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The lichenicolous Coelomycetes

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Contents

Synopsis

A revision of all Coelomycetes so far described from lichens is presented. Twenty genera are accepted, of which 16 are exclusively lichenicolous; seven of these are described as new and an additional new genus is introduced for the lignicolous *Levieuxia borealis* P. Karsten. Forty-two species are treated, including seven new species and seven new combinations; two additional new combinations are made for excluded taxa. A summary of the information on the anamorphs of 21 lichenicolous ascomycetes not considered in detail is included. Fifty epithets, including the type species of ten genera, are excluded

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for a variety of reasons. Keys to the accepted genera and species are provided, as are indexes to both the lichen hosts and fungi reported as growing on them.

Introduction

Remarkable progress has been made in the last three years in synthesizing the available information on the Coelomycetes, fungi producing conidia within flask-like (pycnidia) or disc-like (acervuli) sporocarps (conidiomata). Sutton (1977) assessed the status of the 1336 generic names proposed for Coelomycetes up to that time and was able to reject 720 for a variety of reasons. Synoptic keys to 200 genera were provided by Michaelides *et al.* (1979), and Sutton (1980) has prepared an exhaustive treatment of 375 accepted genera, including numerous line drawings and keys. Despite uncertainty in the application of 226 generic names, it is now possible to approach the Coelomycetes from a firmer taxonomic base than has hitherto been possible.

It is against this background that the present revision of the Coelomycetes now known from lichens is presented. As in the case of my companion treatment of the lichenicolous Hyphomycetes (Hawksworth, 1979), this work is not to be interpreted as a definitive monograph. Rather, it should be viewed as a summation and re-assessment of the available information to provide a starting point for future work on this group of lichenicolous fungi.

Vouaux (1914: 191–198, 281–301) treated 16 genera of lichenicolous Coelomycetes, comprising 52 species, world-wide. Keissler (1930: 534–589) accepted 42 species in central Europe distributed through 19 genera. In the compilation of Clauzade & Roux (1976: 77–89), 54 species were distributed through 19 genera, although it should be stressed that their publication overlooked some previously published generic and specific names. Even at this late date, arbitrary nineteenth century generic concepts, ignoring methods of conidiogenesis and critical study of conidiomata, were still being employed. Furthermore, the identities of all but a handful of taxa had never been illustrated nor re-examined since their original description.

In the course of the last few years, I have investigated a number of lichenicolous Coelomycetes (Hawksworth, 1975*a*, 1976, 1977, 1978*a*, 1980*a*; Hawksworth & Dyko, 1979; Hawksworth & Punithalingam, 1973). The present work represents a culmination of my studies on these fungi by considering all names previously described as lichenicolous Coelomycetes and, further, by taking the opportunity to describe some hitherto unrecognized genera and species.

Biological and taxonomic concepts

Biological concepts

Very few, if any, lichens appear to have anamorphs (imperfect states) referrable to the Hyphomycetes (Vobis & Hawksworth, 1981), so the separation of the normal anamorphs of the host from Hyphomycetes also present does not create any special problems. In the case of the Coelomycetes the situation is very different. Pycnidial anamorphs are known in perhaps as many as 8,000 lichens and these have repeatedly been misinterpreted as lichenicolous fungi; six generic and 19 species names are excluded here as definitely or probably based on the normal pycnidia of the host (pp. 74–89).

There is a considerable degree of variation between the coelomycete anamorphs of lichens depending on the order to which they belong (Vobis & Hawksworth, 1981; Vobis, 1980). However, these structures have been little studied by lichenologists and only in the last few years have they started to be described more fully in species descriptions. Fortunately there are a few early papers which include careful drawings of a wide range of lichen pycnidia (Tulasne, 1852; Lindsay, 1859, 1872; Glück, 1899; Galløe, 1927–1972); it is essential when

working on lichenicolous Coelomycetes to have these works to hand, and also to check herbarium specimens in the case of undocumented taxa. This is especially important when the invading fungus does not cause any visible damage to the host (i.e. is parasymbiotic). If necrotic patches, gall-like growths, or discolourations occur, or the pycnidia are within the hymenium or discrete local patches, it is fortunately normally safe to assume that a lichenicolous fungus is involved.

In some cases the normal pycnidia may function as spermatia, but at least in some groups the conidia are evidently able to germinate to form extensive mycelia (Vobis, 1977). For descriptive purposes it is, following usage in other ascomycetes, now usual to use the terms 'pycnidia' and 'conidia' as morphological ones not implying function. There seems to be no reason to depart from this procedure when considering lichen-forming fungi.

Some lichens regularly occur in the pycnidial state (e.g. *Cliostomum griffithii* (Sm.) Coppins) and there are examples where only pycnidia and no ascocarps are known (e.g. *Lecanactis subabietina* Coppins & P. James; Coppins & James, 1979); in the latter case the species are referred to genera defined on the ascosporic state only on the basis of similarities in the pycnidia and chemical products. Some knowledge of these cases is prerequisite to investigations into the lichenicolous Coelomycetes if unfortunate errors are not to be introduced. The situation is further complicated by the recent report of a probably dioecious lichen, *Lecidea verruca* Poelt (Poelt, 1980), and the probable existence of some true lichen-forming Coelomycetes. Many genera of the latter have been described, particularly from South America, but most merit re-investigation (Vobis & Hawksworth, 1981); one is treated as a synonym of *Vouauxiella* here (p. 64) and it is possible that some others also really represent lichenicolous fungi. One taxon described in the present revision, *Nigropuncta rugulosa* (p. 46), might conceivably be a lichen-forming coelomycete.

Additional complexities arise from the occurrence of pycnidial anamorphs in lichenicolous ascomycetes. These have so far been described for very few such fungi, and usually very inadequately. Many more are to be expected to be recognized as the lichenicolous ascomycetes become better known. In the course of this revision I have not made a critical search for these and describe in full only a few which can be found without the teleomorph (ascosporic phase). The results of a preliminary literature survey are, however, included for completeness (pp. 71–74) as some of these reputed anamorphs can be expected to occasionally occur alone.

The above considerations will make it clear that the production of a definitive account of obligately lichenicolous Coelomycetes will probably not be possible until (1) much more is known of the anamorphs of lichen-forming ascomycetes, (2) those of lichenicolous ascomycetes, and (3) an unequivocable basis for separating lichen-forming Coelomycetes from parasymbiotic lichenicolous taxa on 'unknown' thalli emerges. I doubt that the latter will ever be achieved in view of the complexity of fungus-alga interrelationships (Hawksworth, 1978*b*). Fortunately, as stated at the start of this section, it is only where the invading fungus does *not* cause necrotic patches, discolourations, or gall-like growths that such biological demarcation problems arise.

The lichenicolous Coelomycetes causing damage to the host can clearly be interpreted as parasitic (e.g. *Lichenoconium erodens*), but when the host is little affected with no discolouration or damage to the algal cells the situation is better referred to as parasymbiotic. In some instances (e.g. *Pyrenotrichum splitgerberi*) the invading fungus may depress ascocarp production in the host, have evenly scattered conidiomata, and appear lichenized itself; such instances may perhaps be compared to the production of one lichen by the usurping of the algae from a pre-existing lichen colony (Hawksworth *et al.*, 1980).

Gall formation, especially well marked in the case of some lichenicolous Coelomycetes on *Cladonia* (e.g. *Bachmanniomyces uncialicola, Epicladonia sandstedei*), may be viewed as an example of parasymbiosis in which the fungus has an important role in morphogenesis. Galls appear to be particularly common in *Cladonia* where they can be induced by a wide range of fungi and perhaps also other organisms. Painstaking surveys of *Cladonia* galls were prepared by Bachmann (1927*a*, 1927*b*, 1928*a*, 1928*b*, 1929), but they occur more rarely in many

other genera also (Grummann, 1960). The causal agents of many lichen galls currently remains obscure; as knowledge of the lichenicolous fungi increases more may be related to individual species, but in some cases it may be a host reaction to invasion by disparate taxa which is being observed (cf. Hawksworth, 1980*b*: 174).

In my revision of the obligately lichenicolous Hyphomycetes (Hawksworth, 1979: 186), 18 species were excluded as saprophytes found on dead or decaying thalli; several of these were ubiquitous fungi known from an extremely wide range of substrates. In the case of the Coelomycetes found on lichens this does not at present appear to produce any difficulties. As far as I am aware no coelomycete species also known from other substrates has yet been found on either healthy or decaying lichen thalli.

Taxonomic concepts

The characters of value for the delimitation of genera in Coelomycetes have already been discussed in detail by Sutton (1973, 1980), whose works should be consulted for full information on this aspect. It is, however, necessary to draw attention to two particular areas of difficulty. During the last 15 years there has been an increasing emphasis on the method of conidiogenesis in the delimitation of genera of Coelomycetes. However, while the increased precision in the description of taxa is welcome and long overdue, in practice conidiogenesis in Coelomycetes is often much more difficult to study than in many Hyphomycetes as the conidiogenous cells tend to be very much smaller. When working close to the limits of resolution of light microscopy, it is all too easy to be misled; ultrastructural studies have demonstrated this in several cases. It is further becoming clear that some differences which have been given considerable taxonomic weight are not as clearly demarcated at the ultrastructural level as was at first presumed; the outstanding example in this case is the annellide/phialide separation (Sutton, 1980: 20; Vobis & Hawksworth, 1981). Similar difficulties in the Hyphomycetes led Malloch (1979) and Kendrick (1980) to assert that too much emphasis should not be accorded to minor differences in conidiogenesis in otherwise very similar taxa. In the case of the Coelomycetes such caution is also required and I have endeavoured to bear this in mind in the present revision, as in my earlier account of *Lichenoconium* where the problem was also recognized (Hawksworth, 1977: 161).

Sutton (1980) endeavoured to separate pycnidia-like conidiomata into two main types: simple (unilocular) eustroma when composed of a mass of fungal cells or closely interwoven hyphae, reserving 'pycnidia' for ostiolate, brown, thin-walled structures with walls composed of angular pseudoparenchymatous cells (textura angularis). Wall structure is an extremely important, but until recently largely overlooked, character in the Coelomycetes as in many Pyrenomycetes and Loculoascomycetes. Particular attention has consequently been accorded to this feature in the present study. The introduction of increasing numbers of terms for superficially similar but ontogenetically or structurally distinct sporocarps in the ascomycetes is now starting to be rejected, and it therefore seems unwise for coelomycete terminology to pass a similar course. In this account, 'pycnidium' is consequently retained for all globose or flask shaped conidiomata regardless of the wall structure; the nature of the walls is of course indicated in the generic and species descriptions.

Conidial shape, colour, septation, ornamentation, and whether extruded in mucous or dry, are all important characters which, taken in conjunction with others, support generic distinctions. It is, however, becoming clear that the abilities of conidia to develop additional septa or become slightly pigmented do not provide a sound basis for generic separations on their own. In general, such features are rather of specific importance and these, taken together with their size and any differences in pycnidial sizes or aggregation, provide the species concept in most genera treated here.

The ability of a fungus to occur on a particular host does not provide a specific criterion if all other features are similar. For example, *Cornutispora lichenicola* was originally described from *Parmelia sulcata* but is now also known from *Lobaria pulmonaria, P. borreri, P. glabratula* subsp. *fuliginosa, Platismatia glauca,* and *Rhizoplaca chrysoleuca* (see p. 14);

Vouauxiomyces truncatus was thought to be restricted to *P. caperata* but has since been found on *P. perlata* (see p. 71). Where occurrences on different hosts are related to differences in conidial or pycnidial size or other features they can of course support species separations, as in the distinction of *V. santessonii* from *V. truncatus*.

Reaction of the host to infection was recognized by Santesson (1949) as an important supporting feature at the species level in the taxonomy of lichenicolous fungi. This has already proved of value in *Lichenoconium* where species differing in pycnidial, conidiogenous cell, or conidial sizes give rise to dissimilar symptoms on the same host lichen (Hawksworth, 1977; Christiansen, 1980).

It is with some hesitation that I introduce eight new generic names in this work, especially as I have already described three additional genera of lichenicolous Coelomycetes and resurrect two (*Libertiella* and *Lichenosticta*) not treated in recent reviews of coelomycete genera. However, this was to have been expected as (1) most lichenicolous fungi in other groups belong to obligately lichenicolous genera, and (2) the lichenicolous Coelomycetes have been largely ignored by earlier students of both lichenicolous fungi and other Coelomycetes. Additional obligately lichenicolous coelomycete genera certainly remain to be collected and described. Indeed, I have several unnamed specimens which probably represent new genera but are too scant to permit their thorough examination and description. At the same time it is possible that 'intermediate' species may be discovered necessitating the union of some genera accepted here (e.g. *Laeviomyces* and *Lichenodiplis*) and others may merit transfer to independent genera (e.g. *Pseudoseptoria usneae*, *Vouauxiella uniseptata*).

In the case of discovery of a lichenicolous coelomycete which does not appear in this revision, it must be stressed that before deciding it is undescribed it is of paramount importance to establish (a) that it is not the normal pycnidia of the host, and (b) examine the literature on other Coelomycetes (especially Sutton, 1973, 1980) to see if it can be accommodated into another not obligately lichenicolous genus (as is the case with e.g. *Ascochyta lichenoides*, *Cornutispora lichenicola*, *Phoma* species).

Glossary

Most terms which may be unfamiliar to lichenologists are defined in Hawksworth (1979: 289–290); this glossary should be supplemented by that of Sutton (1980: 642–645) for additional terms peculiar to the Coelomycetes.

Methods

In order to ascertain the names of Coelomycetes described from lichens, the literature searches carried out for my survey of the lichenicolous Hyphomycetes were repeated (see Hawksworth, 1979: 189). Undoubtedly some taxa have been inadvertently overlooked, but I endeavoured to make this aspect of the work as thorough as possible so that the present revision can serve as a starting-point for further investigations on these fungi.

Specimens supporting the various published reports were traced wherever possible and the material re-examined, supplemented by other collections available. Type or other material was obtained from the following herbaria in the course of this study: Angers, B, BM, E, GZU, H, IMI, K, LPS, M, PC, S, UPS, URM, SIENA, W, herb. Hafellner, herb. Poelt, and herb. Vouaux (the latter with Prof. Y. Rondon at Marseille). Herbarium abbreviations follow Holmgren & Keuken (1974). An exclamation mark (!) indicates that I have examined the specimen cited.

The microscopic techniques used for the lichenicolous Hyphomycetes (see Hawksworth, 1979: 189–190) were employed; the temporary erythrosin mountant was especially useful for the study of conidiogenous cells. Sections cut at 10 μm with a freezing microtome were examined for almost all taxa discussed. During the latter part of this work I have been fortunate in being able to use an Olympus BH microscope fitted with Nomarski differential

interference contrast, drawing tube, and camera. The need for good optical equipment in studies on Coelomycetes cannot be over-emphasised.

The scanning electron microscope has already proved a valuable aid in the study of those lichenicolous Coelomycetes with ornamented conidia (Hawksworth, 1977; Hawksworth & Dyko, 1979), but no new scanning electron micrographs are included here.

Key to the genera

This is an entirely artificial key to the genera accepted in this revision. It does not include anamorphs of lichenicolous ascomycetes which normally occur in association with the teleomorph (perfect state), information on which is summarized separately (pp. 71–74). In the case of genera which are not obligately lichenicolous, the key is designed only to allow for the known lichenicolous taxa within them.

1	Conidiomata pycnidial	2
–	Conidiomata acervular or superficial and helmet-shaped	21
2(1)	Conidia shades of brown	3
–	Conidia hyaline	7
3(2)	Conidia arising singly	4
–	Conidia arising in long chains	6
4(3)	Conidia unicellular	5
–	Conidia 1-septate	**Lichenodiplis** (p. 37)
5(4)	Conidia verruculose or echinulate; conidiogenous cells ± hyaline; pycnidial walls dark brown	**Lichenoconium** (p. 33)
–	Conidia smooth-walled; conidiogenous cells brownish; pycnidial walls subhyaline	**Laeviomyces** (p. 26)
6(3)	Conidia unicellular and smooth-walled, *or* 1-septate and rough-walled	**Vouauxiella** (p. 64)
–	Conidia multicellular, muriform, rough-walled	**Nigropuncta** (p. 46)
7(2)	Conidia unbranched	8
–	Conidia with a distinct stem and two apical arms	**Cornutispora** (p. 14)
8(7)	Conidia septate	9
–	Conidia unicellular	12
9(8)	Conidia 1-septate	10
–	Conidia 3-septate; conidiogenous cells subglobose to short-ampulliform, polyphialidic	**Keissleriomyces** (p. 25)
10(9)	Pycnidial wall hyphal or composed of sclerenchymatous cells	11
–	Pycnidial wall pseudoparenchymatous; conidiogenous cells phialidic, 4–8 × 2·5–3 μm; conidia rounded at both ends, narrowly ellipsoid, 8·5–10 × 3–4 µm	**Ascochyta lichenoides** (p. 8)
11(10)	Pycnidia superficial, shades of orange, with sclerenchymatous walls; conidiophores elongate and branched	**Karsteniomyces** (p. 22)
–	Pycnidia immersed to erumpent, brown to black, with hyphal walls; conidiophores short, usually absent	**Epicladonia** (p. 15)
12(8)	Conidiogenous cells arising singly, conidia acrogenous (borne only at the apex)	13
–	Conidiogenous cells arising in irregularly branched chains, conidia acro-pleurogenous (borne both apically and laterally); conidia lacriform	**Lichenosticta** (p. 38)
13(12)	Conidia bacilliform, ellipsoid or obpyriform, rounded or truncated at the base	14
–	Conidia lens-shaped to pyriform, pointed at the ends, adhering in mucilage	**Bachmanniomyces** (p. 10)

14(13) Pycnidia brown or black, superficial or immersed 15
– Pycnidia whitish to pale orange, with a deep reddish-brown ring around the ostiole, superficial . . . . **Libertiella** (p. 30)

15(14) Conidia distinctly truncated at the base; conidiogenous cells holoblastic 16
– Conidia with a rounded base; conidiogenous cells enteroblastic (phialidic) . . . 18

16(15) Conidia elongate-ellipsoid or obpyriform 17
– Conidia cymbiform . . . . **Pseudoseptoria** (p. 57)

17(16) Conidia obpyriform; pycnidial wall pseudoparenchymatous . . **Vouauxiomyces** (p. 67)
– Conidia elongate-ellipsoid; pycnidial wall hyphal . . . . **Epicladonia** (p. 15)

18(15) Pycnidial wall entire, cells around the ostiole not separating 19
– Pycnidial base formed by the conidiogenous cells alone, cells around the ostiole readily separating . . . . **Minutophoma** (p. 44)

19(18) Conidiogenous cells subcylindrical or elongate-ampulliform 20
– Conidiogenous cells subglobose to short-ampulliform . . . . **Phoma** (p. 49)

20(19) Pycnidial wall ± smooth; conidia subglobose or narrowly ellipsoid . . **Microcalicium** [anamorphs] (p. 41)
– Pycnidial wall with pointed cells projecting from it; conidia bacilliform . . . . **Asterophoma** (p. 8)

21(1) Conidiomata helmet-shaped, superficial; conidia simple, multiseptate, *or* to 4-branched . . . . . . **Pyrenotrichum** (p. 59)
– Conidiomata scarcely developed, acervular; conidia with *c.* 50 radiating multiseptate arms . . . . **Psammina** (see Hawksworth, 1979: 244–246)

Accepted species

The accepted genera and species have been arranged alphabetically for ease of reference. In the case of genera including more than a single obligately lichenicolous species, keys to the species are included after the account of the genus itself. Descriptions and full synonymies for taxa I have previously treated elsewhere are generally omitted, but references to full descriptions, illustrations, etc., are provided. Synonyms not repeated from these works have been included in the Fungus index (pp. 95–98). Where genera include both lichenicolous and non-lichenicolous species, the generic diagnoses cover the genus as a whole and are partly based on those provided by Sutton (1980).

I. ASCOCHYTA Lib.

Pl. Crypt. Ard., fasc. **1** : 8 (1830).

See Sutton (1980 : 408) for generic nomenclature.

Conidiomata pycnidial, arising singly or in small groups, globose, immersed, brown to dark brown, ostiolate; walls composed of a few layers (often 1–3) of cells, cells pseudoparenchymatous, pale to dark brown, rather thin-walled, textura angularis. *Conidiophores* absent. *Conidiogneous cells* enteroblastic, lining the pycnidial cavity, acrogenous, short-cylindrical to doliiform, phialidic, not proliferating, hyaline. *Conidia* arising singly, not catenate, narrowly ellipsoid or subcylindrical, rounded at the apex but often with a somewhat truncated base, hyaline, 1-septate when mature (exceptionally becoming 2-septate), sometimes distinctly guttulate, thin-walled, smooth-walled.

Type species: Ascochyta pisi Lib.

Number of species: About 350 species are currently accepted but there are many more names in the literature. Taxa in the genus have generally been separated on a host basis in the past, and thorough revisions are required on the lines of that of Punithalingam (1979)

concerning the graminicolous species. Most species occur as leaf and stem-spotting fungi; only a single lichenicolous species is referred to this genus here.

Observations: For practical purposes this genus may be viewed as a 1-septate counterpart of *Phoma* (see p. 49), which it resembles closely in all other respects. As noted by Sutton (*loc. cit.*), attempts to separate these two genera on the basis of ultrastructural differences in conidiogenesis are difficult to relate to light-microscopical observations.

1. Ascochyta lichenodes (A. L. Sm.) D. Hawksw., *Notes R. bot. Gdn Edinb.* **36 :** 182 (1978).

For illustration and further discussion of this species see Hawksworth (*loc. cit.*).

Host: Indeterminate sterile crustose lichen on bark.

Distribution: British Isles (England). Known only from the original collection.

II. ASTEROPHOMA D. Hawksw. gen. nov.

Genus lichenicola ad Coelomycetes Sphaeropsidales pertinens. Conidiomata singularia, uniloculata, dispersa vel laxe aggregata, globosa, superficialia vel hemi-superficialia, atrobrunnea vel nigra, ostiolata, cum muris atrobrunneis e cellulis elongatis pseudoparenchymaticis externe attenuatis et erumpescentis. Conidiophora desunt. Cellulae conidiogenae enteroblasticae, acrogenae, anguste ampulliformes vel late subcylindrices, phialidicae, interdum biphialidicae, non prolifericae, hyalinae. Conidia subcylindrica, hyalina, simplicia, laevia, minutissima, in muco aggregata.

Conidiomata pycnidial, arising singly, uniloculate, scattered or loosely aggregated, globose, superficial or half-immersed, dark brown to black, ostiolate; walls composed of radially orientated elongated dark brown pseudoparenchymatous cells becoming attenuated and projecting slightly at the exterior to give the whole a star-like appearance. *Conidiophores* absent. *Conidiogenous cells* enteroblastic, interdigitated with the inner wall cells and lining the pycnidial cavity, acrogenous, narrowly ampulliform to broadly subcylindrical, phialidic, occasionally biphialidic, not proliferating, hyaline. *Conidia* subcylindrical, hyaline, simple, smooth-walled, minute, aggregated into a slimy mass which is extruded through the ostiole as a whitish drop.

Type species: Asterophoma mazaediicola D. Hawksw. (holotypus).

Number of species: Monotypic.

Observations: This new genus recalls *Minutophoma* (see p. 44) in the minute conidiomata and subcylindrical conidia, but differs in the entire conidiomatal wall, presence of an ostiole, the externally attenuated wall cells, the hyaline conidiogenous cells that are also occasionally biphialidic, and the conidia being extruded in a mucilaginous whitish drop. It does not appear to have any other close allies.

1. Asterophoma mazaediicola D. Hawksw. **sp. nov.**
(Fig. 1A–D)

Fungus lichenicola. Conidiomata singularia, uniloculata, dispersa vel laxe aggregata, globosa, superficialia vel hemi-superficialia, atrobrunnea vel nigra, 30–42 μm diam, ostiolata, cum muris textura angulari 7–10 μm latis e cellulis atrobrunneis elongatis et externe attenuatis et erumpescentis 5–8 × 2–4 μm. Conidiophora desunt. Cellulae conidiogenae enteroblasticae, acrogenae, anguste ampulliformiae vel late subcylindrices, phialidicae, interdum biphialidicae, non prolifericae, hyalinae, 5–7 × 2·5–3·5 μm. Conidia subcylindrica, hyalina, simplicia, laevia, 1·5–3(-3·5) × 0·5–1·5 μm, in muco aggregata.

Typus: Italia, Mendelgebirge, Nordhänge des Roen, inter Mendel-Pass et Marga di Romeno, in mazaediis *Caliciis trabinellae* Ach., 24.x.1976, *J. Hafellner* 1822 (herb. Hafellner—holotypus!).

Conidiomata pycnidial, superficial or partly immersed, arising in the mazaedial ascospore mass of the host, arising singly but sometimes loosely aggregated and juxtaposed, to 12 in a single mazaedium, dark brown to black, 30–42 μm diam, ostiolate; wall 7–10 μm thick, composed of a layer of radially elongated dark brown pseudoparenchymatous cells becoming

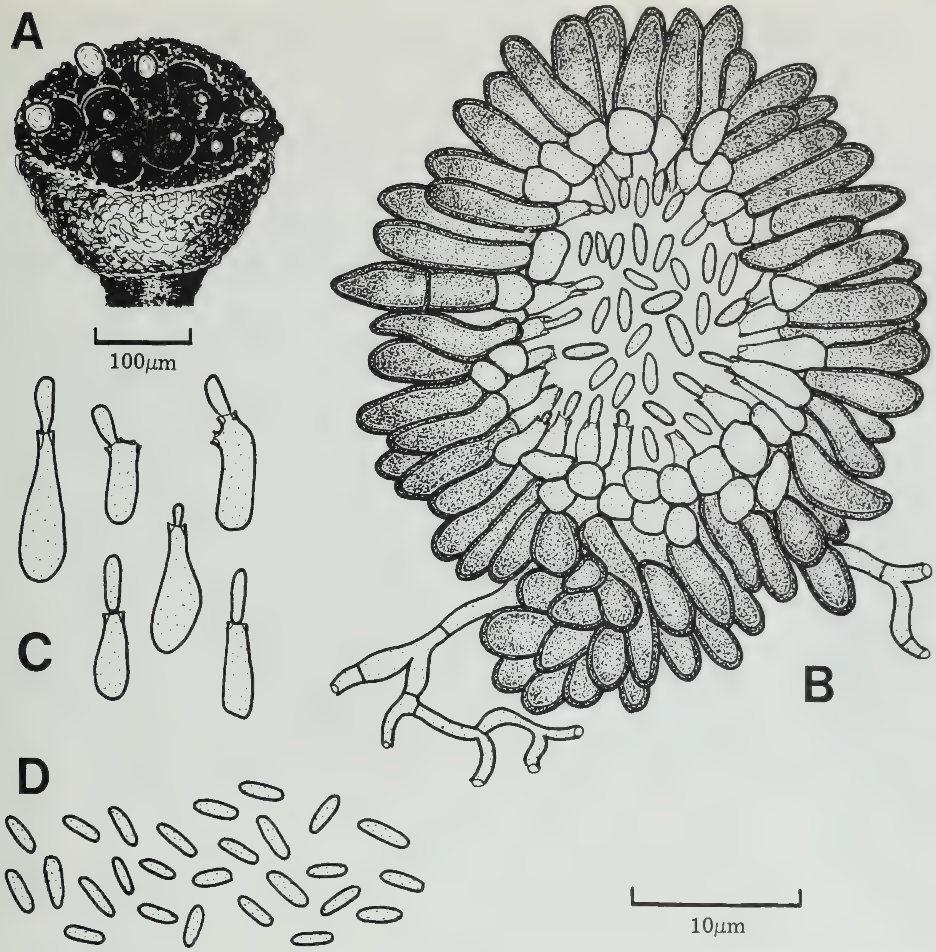

Fig. 1 *Asterophoma mazaediicola* (herb. Hafellner—holotype). **A,** Infected mazaedium with pycnidia extruding conidia in mucilaginous drops. **B,** Vertical section of pycnidium. **C,** Conidiogenous cells. **D,** Conidia.

attenuated and projecting slightly at the exterior to give the whole a star-like appearance, 5–8 × 2–4 μm, lined internally with smaller subhyaline to hyaline subglobose to polyhedral pseudoparenchymatous cells 1·5–3·5 μm diam; mycelium ramifying through the mazaedium, hyphae hyaline, uneven in diameter, septate, irregularly branched, mainly 1·5–2·5 μm thick. *Conidiogenous cells* enteroblastic, interdigitated with the inner wall cells lining the pycnidial cavity, difficult to distinguish, acrogenous, narrowly ampulliform to broadly subcylindrical, rather variable in shape, phialidic, occasionally biphialidic with two conidiogenous loci per cell, not proliferating, hyaline, 5–7 × 2·5–3·5 μm. *Conidia* abundantly produced, subcylindrical, rounded at the apices, hyaline, simple, smooth-walled, not distinctly guttulate, 1·5–3(-3·5) × 0·5–1·5 μm, aggregated into a slimy mass which is extruded through the ostiole as a whitish drop.

Hosts: Calicium glaucellum Ach. and *C. trabinellum* Ach., apparently confined to mazaedial ascospore masses. Especially frequent on *C. trabinellum.* Evidently a mild pathogen as diseased fruits often appear stunted and bent; the amount of vulpinic acid pigment produced by *C. trabinellum* also appears to be reduced in diseased specimens so that such collections can easily be misidentified as *C. glaucellum.* The absence of records from other *Calicium* species suggests that the fungus has a very narrow host range; indeed *C. glaucellum* and *C. trabinellum* are extermely close to one another and conceivably

chemotypes of a single taxon (Tibell, 1975 : 106). Infected fruits are easily recognized by the verrucose surface that derives from the pycnidia themselves and particularly by the extruded white mucilaginous drops containing the conidia.

Distribution: Canada, France, Italy, Norway, Rwanda, Sweden and the U.S.A. Probably scattered throughout the range of its host species (i.e. circumboreal), to judge from material so far available, and locally abundant.

Observations: A distinctive species easily recognized by its very specialized habitat. The pycnidia of *Microcalicium subpedicellatum* (p. 42) are larger (40–60 μm diam), with a totally different wall structure, longer phialides, broadly ellipsoid to subglobose conidia, and occur only on the thalli (not in the mazaedium); *M. subpedicellatum* is known from *Calicium glaucellum* (Tibell, 1978 : 244) but has not been reported from *C. trabinellum*. The pycnidia of these *Calicium* species, when present, only occur on the thallus, not the mazaedium, and produce larger conidia *c.* 4–5 × 1·5 μm (fide L. Tibell, *in litt.*).

Additional specimens: **Canada:** British Columbia: Glacier National Park, Highway 1, 7 km NE of Rogers Pass, on *Calicium glaucellum*, 6 September 1972, *L. Tibell* 4959 (UPS!); Wells Gray National Park, Helmcken Falls, on *C. glaucellum*, 19 September 1972, *L. Tibell* 5185 (UPS!); Pemberton Valley, *c.* 20 miles N of Pemberton, on *C. glaucellum*, 17 September 1972, *L. Tibell* 5180 (UPS!). —**France:** Haute Savoie : Chamonix, 0·5 km S of Planpra, Plan des Chablettes, on *C. trabinellum*, 27 August 1970, *L. Tibell* 4375 (UPS!); 1·5 km SSE of Chamonix, on *C. trabinellum*, 26 August 1970, *L. Tibell* 4383 (UPS!). —**Italy:** Trentino-Alto Adige : Ortlegruppe, Martelltal, on *C. trabinellum*, 2 October 1971, *L. Tibell* 4466 (UPS!). —**Norway:** Hedmark, Engerdal par., 3·5 km SW of Hovdroseter, on *C. trabinellum*, 29 July 1973, *L. Tibell* 5548 (UPS!). —**Rwanda:** Chaine des Birunga, Versant S of Bisoke, on *C. trabinellum*, 25 February 1972, *J. Lambinon* 72/RW/883 (LG n.v., *fide* Tibell, *in litt.*). —**Sweden:** Åsele Lappmark : Frederika par., Vargån, 1·8 km SW of Flakaträsk, on *C. trabinellum*, 5 August 1972, *L. Tibell* 4612 (UPS!). Dalarna : Hamra par., Hamra National Park, on *C. trabinellum*, 20 July 1973, *L. Tibell* 5433 (UPS!), 5448 (UPS!); *loc. cit.*, on *C. glaucellum*, 20 July 1973, *L. Tibell* 5424 (UPS!). Härjedalen: Ljusnedal par., 6 km NNE of Ljusnedal, Ormberget, on *C. trabinellum*, 25 July 1973, *L. Tibell* 5503 (UPS!). Jämtland: Fors par., 10 km NNW of Fors, on *C. trabinellum*, 2 August 1977, *L. Tibell* 7262 (UPS!). Norbotten: Överkalix par., 39 km NW of Överkalix, mire between Svartberget and Ö. Näverberget, on *C. trabinellum*, 14 July 1977, *L. Tibell* 6762 (UPS!). Lule Lappmark: Muddas National Park, 5 km E of Porjus, on *C. glaucellum*, 21 July 1977, *L. Tibell* 6962 (UPS!); *loc. cit.*, at the little stream N of Muddusfallet, on *C. trabinellum*, 21 July 1977, *L. Tibell* 7026 (UPS!). Uppland: Vänge par., Fiby urskog, on *C. glaucellum* 22 March 1964, *L. Tibell* 2044a (UPS!). —**U.S.A.:** Michigan : Keweenaw Co., Isle Royale, Rasberry Island, outside Rock Harbor, on *C. trabinellum*, 24 August 1972, *L. Tibell* 4656 (UPS!).

III. **BACHMANNIOMYCES** D. Hawskw. **gen. nov.**

Genus lichenicola ad Coelomycetes Sphaeropsidales pertinens. Conidiomata singularia, uniloculata, dispersa, globosa vel subglobosa, immersa, hyalina sed ostiolis aurantiacis vel brunneis, cum muris textura intricatis, ostiolata. Conidiophora desunt. Cellulae conidiogenae holoblasticae, acrogenae, elongato-ampulliformes, prolifericae, annellatae, hyalinae. Conidia late fusiformia ad pyriformia, plerumque asymmetrica, hyalina, simplicia, laevia, in mucosa.

Conidiomata pycnidial (eustromatic), arising singly, scattered, globose to subglobose, immersed, hyaline but orange to brownish at the ostiole; walls composed of moderately thick-walled compactly entwined hyphae forming a textura intricata, hyaline except near the ostiole. *Conidiophores* absent. *Conidiogenous cells* holoblastic, lining the inner wall of the pycnidial cavity, acrogenous, elongate-ampulliform, somewhat broader at the base and tapering above, proliferating, annellate, hyaline, unbranched, occasionally septate. *Conidia* slimy and adhering together, not catenate, lens-shaped to pyriform, attenuated at the apices, the base narrowly truncate at the point of secession, often asymmetric, hyaline, simple, smooth-walled.

Type species: Bachmanniomyces uncialicola (Zopf) D. Hawksw. (syn. *Phyllosticta uncialicola* Zopf—holotypus).

Fig. 2 *Bachmanniomyces uncialicola* (W 1929/2—holotype of *Sirococcus lichenicola*). **A**, Gall with pycnidia close to the apex of a branch, note the thinner stem above the gall (× 12·5). **B**, Gall with pycnidia arising laterally, the branch similar in thickness above and below the gall (× 12·5).

Number of species: Monotypic.

Observations: Bachmanniomyces has no very close allies amongst the non-lichenicolous Coelomycetes. The conidiogenous cells in *Discosporium* Höhnel (type species *D. populeum* (Sacc.) B. Sutton) are rather similar but the pycnidia in that genus are dark brown and aggregated into stromata. *Sirococcus* Preuss (type species *S. stobilinus* Preuss) was probably selected by Keissler (*in* Bachmann, 1929) for this fungus as he interpreted the conidia as catenate, but in *Sirococcus* the pycnidia are carbonaceous, lack a distinct ostiole, and the conidiogenous cells are branched (see Sutton, 1980).

This new genus is named in honour of Edwald Th. Bachmann (1850–1937) in recognition of his pioneering work on gall-like structures in lichens, including investigations of the type species of *Bachmanniomyces* (Bachmann, 1929).

1. Bachmanniomyces uncialicola (Zopf) D. Hawksw. **comb. nov.**
(Figs. 2A–B, 3A–E)

Phyllosticta uncialicola Zopf, *Hedwigia* **35** : 324 (1896).

Type: British Isles, Scotland, Perthshire, Dunkeld, summit of Birnam Hill, on *Cladonia uncialis*, September 1858, *W. L. Lindsay* (E—lectotype!).

Phoma uncialicola (Zopf) Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 198 (1914).

Sirococcus lichenicola Keissler, *in* Bachmann, *Arch. Protistenk.* **66** : 469 (1929).

Type: Sweden, Åsele Lappmark, Kirchspiel Vilhelmina, auf *Cladonia amaurocraea*, Sommer 1928, *G. Nilsson [G. Degelius]* (W 1929/2—holotype!).

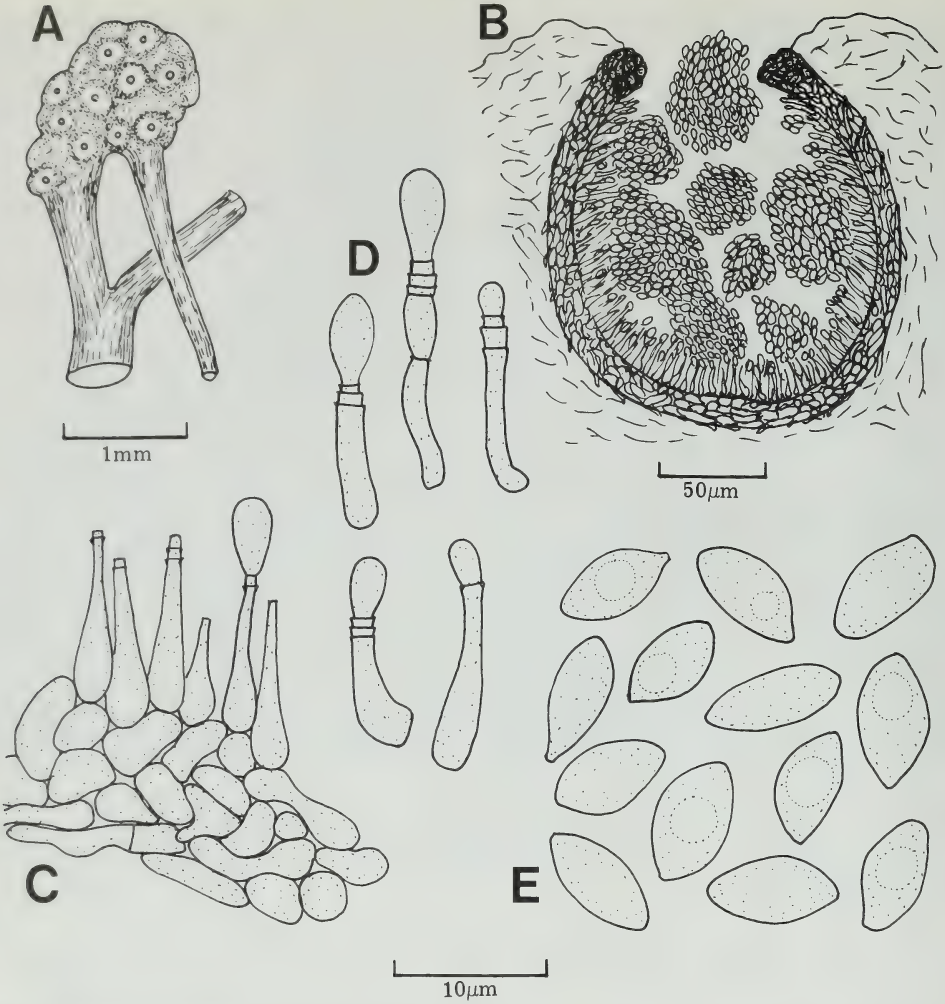

Fig. 3 *Bachmanniomyces uncialicola* (W 1929/2—holotype of *Sirococcus lichenicola*). **A,** Gall on geniculately deformed branch. **B,** Vertical section of pycnidium. **C,** Vertical section of pycnidial wall. **D,** Conidiogenous cells. **E,** Conidia.

*Exsiccatae**: Arnold, *Lich. Exs.* no. 1021a (BM!; sub *Cladonia uncialis* f. *biuncialis*).—Sandstede, *Clad. Exs.* no. 161 (BM!; sub *C. uncialis*), no. 162 (BM!, UPS!; sub *C. uncialis*).—Schaerer, *Lich. Helv.* no. 514 (not found on this number in BM but cited by Sandstede, 1931 : 192; sub *C. stellata β. ceranoides* f. *adusta*).—Zwackh, *Lich. Exs.* no. 695 (n.v., cited by Sandstede, *loc. cit.*: 192; sub *C. uncialis* f. *leprosa*).

Icones: Bachmann, *Ber. dtsch. bot. Ges.* **38** : 335 fig. 6 [?] (1921); *Arch. Protistenk.* **66** : 461 figs 1–2, 462 fig. 3, 465 figs 4–11 (1929).—Keissler, *Rabenh. Krypt.-Fl.* **8** : 537 figs 100–101, 553 fig. 106a (1930).—Lindsay, *Trans. R. Soc. Edinb.* **25** : pl. 7 figs 15–16 (1859).

Conidiomata pycnidial, completely immersed in gall-like deformations of the host, the galls massive irregular convex swellings to 1–1·5 mm diam making the branches on which they occur geniculate, galls concolorous with the thallus, pycnidia arising singly, not aggregated into stromata, evenly scattered over the galls, the ostiole depressed below the surface level of the gall, orange at first but becoming brownish with age, 50–70 μm wide with the opening mainly 40–50 μm wide, pycnidia globose to subglobose, mainly

*Keissler (1930 : 540) cited Sandstede *Clad. Exs.* no. 106; that number is *C. portentosa* Dufour (BM!) and does not support this fungus.

100–200 μm diam when mature; pycnidial wall translucent, hyaline, mainly 12–20 μm thick, becoming slightly more swollen and orange to brownish near the ostiole, the pigmentation due to interstitial mainly extra-hyphal deposition, only the limiting membrane of the hyphae in the ostiolar region coloured, wall throughout formed of irregularly orientated entwined and compacted moderately thick-walled hyphae mainly 2–3 μm wide. *Conidiogenous cells* holoblastic, arising from the inner wall of the pycnidium, completely lining the pycnidial cavity, elongate-ampulliform, the bases often expanded and tapering markedly towards the apex, hyaline, smooth-walled, annellidic with to at least 4 annellations, unbranched, simple or occasionally 1-septate, 7–12 μm tall, mainly 3–4 μm wide at the base and tapering to 2–3 μm at the apex. *Conidia* abundantly produced, not catenate, slimy and adhering together in large groups in aqueous preparations, lens-shaped to pyriform, often asymmetrical, apices often somewhat attenuated, the basal one more markedly so and also abruptly truncate when about 1 μm thick, hyaline, simple, often with a large guttule, smooth-walled, (7–)8–10(–10·5) × 4–5·5(–6) μm.

Hosts: Cladonia amaurocraea (Flörke) Schaerer, *C. terrae-novae* Ahti, and *C. uncialis* (L.) Wigg., thalli. The infection leads to the formation of distinctive galls (see above; Figs 2, 3). The galls are of the same colour as the healthy thallus and healthy algal cells consistently occur in the close proximity of the pycnidia; this fungus consequently appears to form a stable relationship with the host and not to be a pathogen. Vouaux's (1914 : 198) mention of its occurrence on *C. bellidiflora* (Ach.) Schaerer is due to confusion with '*Abrothallus*' *moorei* Lindsay, and his mention of it on *C. stellaris* Opiz may also be incorrect. Keissler's (1930 : 540) reports from *C. ochrochlora* Flörke, '*C. silvatica*' and *C. surrecta* Flörke, and Sandstede's (1931 : 317) from *C. turgida* (Ehrh.) Vainio, require confirmation.

Distribution: British Isles (Scotland), Canada, France, Germany, Italy, Sweden and Switzerland.

Observations: A very detailed account of the galls produced by *Bachmanniomyces uncialicola* is given by Bachmann (1929 : 460–469) who did, however, describe the conidia as forming in chains. I was unable to see any evidence of this, though the conidia strongly adhere in irregular slimy masses which presumably swell when moist and ooze through the rather wide ostioles. If the conidia were catenate, it would be anticipated that the mature ones would have a minute truncate point of secession at *both* ends when in fact this only occurs at their bases. The first-formed conidium arises holoblastically and if a young pycnidium is studied no or few conidiogenous cells with annellations will be found. The annellations are not easy to see in older conidiogenous cells unless studied in erythrosin-ammonia or a similar mountant.

Lindsay (1859 : pl. 7 figs 15–16) was evidently the first author to recognize this fungus. He originally considered it to be a pycnidial state of *Lecidea cladoniaria* Nyl. (syn. *Nesolechia cladoniaria* (Nyl.) Arnold) but later realized that this was not so (Lindsay, 1871 : 28–29). He also discovered an ascomycete on this host, named '*Abrothallus*' *moorei* Lindsay (Lindsay, 1869*a* : 545), and described its conidia which were, however, much longer and narrower than those of *Bachmanniomyces uncialicola.* Vainio (1887 : 265) recognized that deformations of *Cladonia uncialis* named as var. *leprosa* Delise were caused by a lichenicolous fungus, and Harmand (1907 : 245) ascribed this to *Phyllosticta uncialicola* Zopf.

Zopf (1896 : 324) gave an extremely short diagnosis of *Phyllosticta uncialicola:* 'Anschwellung an der Podetien bewirkend. Conidien einzellig, farblos, ei- oder birnformig, 8, 4 : 5' and did not cite any specimens. No material of this taxon could be located in B (B. Hein, *in litt.*) but the original description is so characteristic of the present species that there can be no doubt as to the taxon he intended to describe. However, as Zopf introduced the name in his compendium of lichenicolous fungi then known, it is most unlikely that he overlooked Lindsay's (1859) description and comments on this fungus; Zopf cites these works in the introduction to his list and it is probable that he introduced the name with Lindsay's then unnamed fungus in mind. Lindsay's material is consequently designated

lectotype for Zopf's name here, but the possibility that it was the holotype should not be discounted.

Vouaux (1914 : 198) indicated 'sans doute' that *Spilomium epicladonia* H. Olivier was a synonym of the present species. However, as the conidia of Olivier's fungus were given as 6–8 × 3–4 μm it seems unlikely that this interpretation is correct.

Additional specimens: **Canada:** British Columbia, Queen Charlotte Islands, Graham Island, central part between Boulton Lake and Watun River, 53° 49′ N, 132° 4′ W, on *Cladonia uncialis,* 3 August 1966, *H. Sjörs* (H!). Newfoundland, St. Mary's District, 2 mi E of Peter's River, on *C. terrae-novae,* 7 June 1956, *T. Ahti* 9327 (H!). —**Germany:** Oldenburg, Kaihausermoor in Moorboden, on *C. uncialis,* April 1918, *H. Sandstede* [*Clad. Exs.* no. 162.] (BM!, UPS!); *loc. cit.,* October 1917, *H. Sandstede* [*Clad. Exs.* no. 161.] (BM!). —**Italy:** Höhe zwischen Glashütten und Volsbach, südlich von Bayreuth, auf Sandboden des braunen Jura, on *C. uncialis,* 6 September 1884, *F. G. C. Arnold* [*Lich. Exs.* no. 1021a.] (BM!). —**Sweden:** Uppland, Uppsala, Witulfsberg, on *C. uncialis,* 1852, *Th. M. Fries* (UPS!).

IV. CORNUTISPORA Piroz.

Mycologia **65** : 763 (1973).

Conidiomata pycnidial, arising singly, subglobose, almost translucent to pale brown, immersed to almost superficial, opening by an irregular disintegration of the upper part of the pycnidial wall; walls composed of thin-walled pseudoparenchymatous cells, textura angularis. *Conidiophores* arising from the inner wall of the pycnidial cavity, irregularly branched, septate, smooth-walled, hyaline, conidia forming acropleurogenously. *Conidiogenous cells* polyblastic, integrated, indeterminate, broader towards the apices, hyaline, with 1–4 apical denticles. *Conidia* arising singly, triradiate with a subcylindrical stem, two apical branches diverging at an obtuse angle, and a distinctly narrowed foot-cell, hyaline, simple, smooth-walled.

Type species: Cornutispora limaciformis Piroz.

Number of species: Two; *C. limaciformis,* which occurs in the apothecia of *Therrya fuckelli* (Rehm) Kujala (Phacidiales), and a single lichenicolous species distinguished by its much shorter conidia.

Observations: The conidia of this genus are especially characteristic and it appears to have no close relatives in the Coelomycetes.

1. **Cornutispora lichenicola** D. Hawksw. & B. Sutton, *in* Hawksworth, *Trans. Br. mycol. Soc.* **67** : 51 (1976).
(Fig. 4A–B)

This fungus is described and illustrated in Hawksworth (1976 : 51–53), and further drawings are given by Sutton (1980 : 90), so it is not discussed in detail here.

Hosts: Lobaria pulmonaria (L.) Hoffm. (thallus), *Parmelia borreri* (Sm.) Turner, *P. glabratula* subsp. *fuliginosa* (Fr. ex Duby) Laundon (thallus), *P. sulcata* Taylor (thallus), *Platismatia glauca* (L.) Culb. & C. Culb. (thallus), and *Rhizoplaca chrysoleuca* (Sm.) Zopf (syn. *Lecanora rubina* (Vill.) Ach.) (apothecia). Commonly in mixed infections with other lichenicolous fungi. The host tissues are sometimes blackened, decolourized, or otherwise discoloured, but it is often not clear whether this is due to the *Cornutispora* or the other fungi present.

Distribution: Austria, British Isles (England, Scotland), Italy, and Switzerland.

Specimens (additional to Hawksworth, *loc. cit*): **Austria:** Burgenland: Bez. Oberwart, SW of Bad Tatzmannsdorf, on *Parmelia sulcata,* 7 April 1980, *J. Poelt* (GZU!; with *Lichenoconium usneae*). —**British Isles:** England, S. Devon, Slapton, Slapton Ley Nature Reserve, Peasdish, on *P. borreri,* 28 August 1980, *D. L. Hawksworth 5064* (IMI 251276!; with *L. lecanorae*); S. Somerset, Porlock, Horner Combe, on *Platismatia glauca,* 21 September 1980, *D. L. Hawksworth 5072* (IMI 251490!); S.

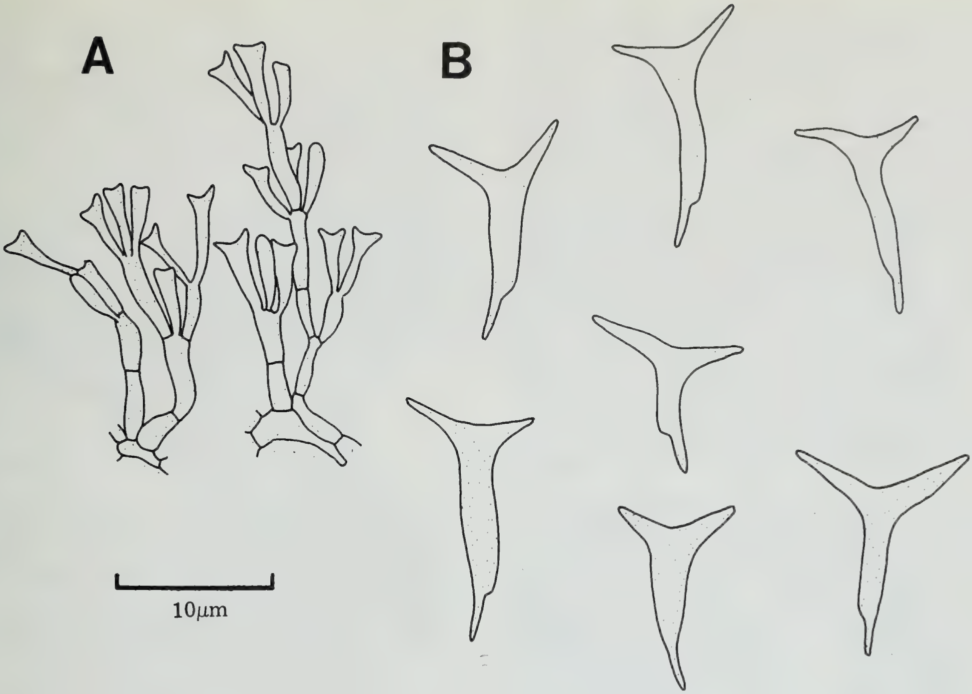

Fig. 4 *Cornutispora lichenicola* (IMI 186831—holotype). **A,** Conidiogenous cells. **B,** Conidia. Reproduced from Hawksworth (1976 : 52).

Somerset, Nettlecombe Park, on *Parmelia sulcata,* 20 September 1980, *D. L. Hawksworth 5069* (IMI 251487!). Scotland, Kintyre, *c.* 7 km SW of Crinan, on islet N of Carsaig Island, on *Lobaria pulmonaria,* 14 August 1977, *N. Brandt* (E!, IMI 224707!; with *Endophragmiella hughesii*). —**Italy:** Südtirol, Ötztaler Alpen, Vinschgau, on *Rhizoplaca chrysoleuca,* 18 October 1975, *J. Hafellner* (GZU!; with *Lichenoconium lecanorae*). —**Switzerland:** Wallis, Aletschwald ob Brig, on *P. glabratula* subsp. *fuliginosa,* 11 September 1968, *J. Poelt* (hb. Poelt 6359!; with *L. usneae*).

V. **EPICLADONIA** D. Hawksw. **gen. nov.**

Genus lichenicola ad Coelomycetes Sphaeropsidales pertinens. Conidiomata singularia, uniloculata, subglobosa, ad cupuliformia, atrobrunnea immersa ad erumpescentia, cum muris textura intricatis, subhyalinis sed atrobrunneis in parte exposito, ostiolata. Conidiophora plerumque desunt. Cellulae conidiogenae holoblasticae, acrogenae, subcylindrices ad elongato-ampulliformes, prolifericae, annellatae, hyalinae. Conidia subcylindrica ad anguste-ellipsoidea vel cymbiformia, hyalina, 0–1 septata, laevia.

Conidiomata pycnidial (eustromatic), arising singly, scattered, subglobose to cupuliform, immersed to erumpent, dark brown; walls composed of compacted entwined short-celled hyphae forming a textura intricata, subhyaline except in the exposed parts, ostiolate. *Conidiophores* usually absent. *Conidiogenous cells* holoblastic, lining the inner wall of the pycnidial cavity, acrogenous, subcylindrical to elongate-ampulliform, proliferating, annellate, usually unbranched, hyaline. *Conidia* arising singly, not catenate, subcylindrical to narrowly ellipsoid or cymbiform, hyaline, 0–1 septate, smooth-walled.

Type species: Epicladonia sandstedei (Zopf) D. Hawksw. (syn. *Diplodina sandstedei* Zopf—holotypus).

Number of species: Three, all of which are only known from *Cladonia* species on which they commonly form galls.

Observations: Epicladonia is distinguished from *Bachmanniomyces,* which also forms galls on *Cladonia* species (p. 10), in that the exposed parts of the pycnidia are dark brown to black, never shades of orange. Furthermore, the conidia are never pyriform nor strongly adhering in mucilage, 1-septate in two species, and have a much broader scar than is seen in *B. uncialicola.* In *Pseudoseptoria usneae* (p. 57), the walls of the pycnidia are of greenish-brown pseudoparenchymatous cells (textura angularis) and the conidiogenous cells tend to be relatively short and stout.

The three species referred to this new genus here are separated primarily on the basis of conidial size and septation and further, for *E. simplex,* the degree of emergence and extent of consequent pigmentation of the pycnidial wall.

It is conceivable that *Verrucaster* Tobler might provide an earlier name for this genus, but in the absence of further information on the type species (see p. 88), I feel it is not possible to take it up here with any degree of confidence.

Key to the species

1 Pycnidia mainly less than 100 μm diam, immersed, brown only immediately around the ostiole 2

– Pycnidia 100–175 μm diam, erumpent and becoming almost superficial, the exposed parts all brown; forming galls; conidia simple, subcylindrical, rounded at the apex, 8·5–11(–12) × 2·5–3(–3·5) μm . . . . **Epicladonia simplex** (p. 19)

2 Conidia predominantly 1-septate, subcylindrical to narrowly ellipsoid, apex always rounded, (7·5–)9–12(–14) × (2·5–)3–4 μm; usually forming galls **Epicladonia sandstedei** (p. 16)

– Conidia predominantly simple, subcylindrical to almost cymbiform, apex often attenuated, 7·5–11 × 3–3·5 μm; not forming galls . . . . . . **Epicladonia stenospora** (p. 20)

1. Epicladonia sandstedei (Zopf) D. Hawksw. comb. nov.
(Figs. 5A–B, 6A–E)

Diplodina sandstedei Zopf, *in* Sandstede, *Abh. naturw. Ver. Bremen* **18** : 429 (1906).
Type: Germany, Oldenburg, Westerstede, 'Erdwalle in der Waldung "Hassen" bei Keilburg', on *Cladonia caespiticia* (Pers.) Flörke [?], *H. Sandstede.*

? *Diplodina claudelii* Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 289 (1914); as '*claudeli*'.
Type: France, Vosges, on *Cladonia* sp., *V. Claudel.*

Exsiccatae: Krypt. Exs. Vindob.* no. 1330*b* (sub *Diplodina sandstedei;* B!, K!). [The fungus was not found on copies of no. 1330[*a*] studied (B!, K!).]

Icones: Keissler, *Rabenh. Krypt.-Fl.* **8** : 18 fig. 11, 19 fig. 13, 25 fig. 20, 570 figs. 109–111 (1930).

Conidiomata pycnidial, normally immersed in galls; galls convex, verruciform, to *c.* 1 mm diam, often somewhat constricted at the base, 5–10(–15) pycnidia in each gall, galls concolorous with the host tissue, not developed in early stages of infection when mature pycnidia can arise directly on the podetia; pycnidia arising singly, not aggregated into stromata, evenly scattered over the galls, immersed, the ostiole and upper part of the pycnidium slightly erumpent, translucent brown to almost black when mature, subglobose at first but becoming gaping and almost cupuliform with age, 50–80(–125) μm diam; ostiole clearly delimited in younger pycnidia, depressed, circular, to *c.* 50 μm diam, centre appearing subhyaline due to the conidial mass, formed by a breakdown of the upper wall of the pycnidium, irregular in shape in older pycnidia; pycnidial walls ± subhyaline except in the vicinity of the ostiole, there olivaceous brown to dark brown, mainly 8–15 μm thick, to 20 μm thick near the ostiole, wall throughout composed of densely interwoven moderately thick-walled hyphae, these short-celled and mainly 2·5–4·5 μm wide, textura intricata but

*Sandstede (1931) lists 24 exsiccatae numbers from seven sets on which he found this fungus. These are excluded as they were issued for the host *Cladonia* and the fungus is probably absent from some copies of these numbers.

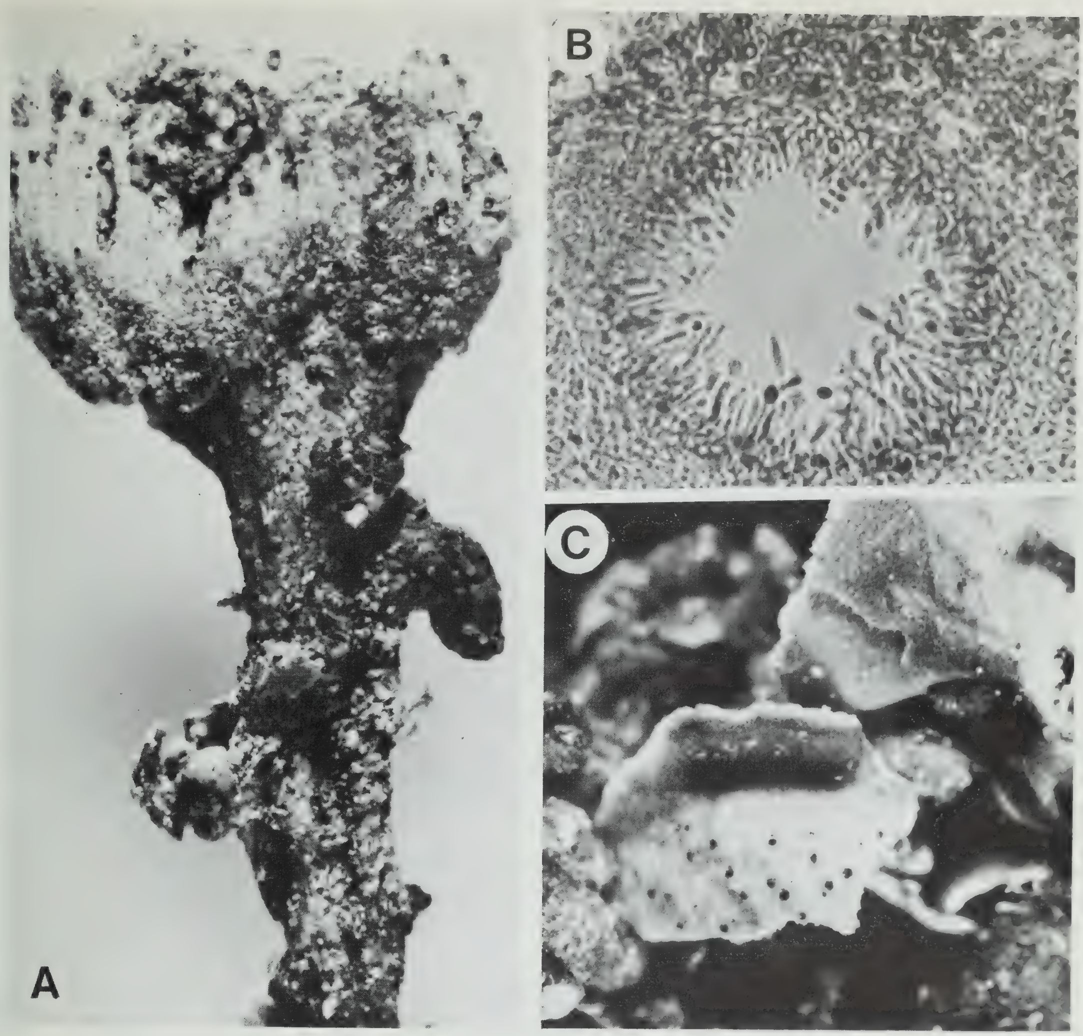

Fig. 5A–B, *Epicladonia sandstedei* (IMI 240228); **A,** infected podetium with galls (× 12·5); **B,** vertical section of pycnidium (× 500). **C,** *E. stenospora (Döbbeler 1827),* infected squamule showing decolorization and pycnidia (× 20).

appearing almost cellular in parts. *Conidiophores* absent or short-cylindrical, simple or sparsely branched at the base, hyaline, variable in length, to 25 μm tall, 3–4 μm wide. *Conidiogenous cells* holoblastic, arising directly from the pycnidial wall or integrated into the conidiophores, subcylindrical to elongate-ampulliform, tapering towards the apex, hyaline, smooth-walled, annellidic, with 0–3 annellations, mainly 10–20 μm tall, 3–4 μm wide at the base, mainly 1·5–2·5 μm wide at the apex. *Conidia* abundantly produced, arising singly, not catenate, subcylindrical to narrowly ellipsoid, rounded at the apex, truncated at the base with a scar 1·5–2 μm wide (remnants of wall tissue sometimes evident at high magnifications), hyaline, (0–)1—septate when mature, 2–3 guttulate, thin-walled, smooth-walled, (7·5–)9–12(–14) × (2·5–)3–4 μm.

Hosts: Cladonia species, squamules and podetia, usually forming irregularly lobed bullate galls which may be hollow inside. Probably parasymbiotic. I have not made an exhaustive study of *Cladonia* specimens in search of the fungus but according to Sandstede (1931) it has a very wide host range. Sandstede mentioned it on *C. anomaea* (Ach.) Ahti & P. James, *C. carneola* (Fr.) Fr., *C. coniocraea* auct., *C. chlorophaea* (Flörke ex Sommerf.) Sprengel *s. lat.*,

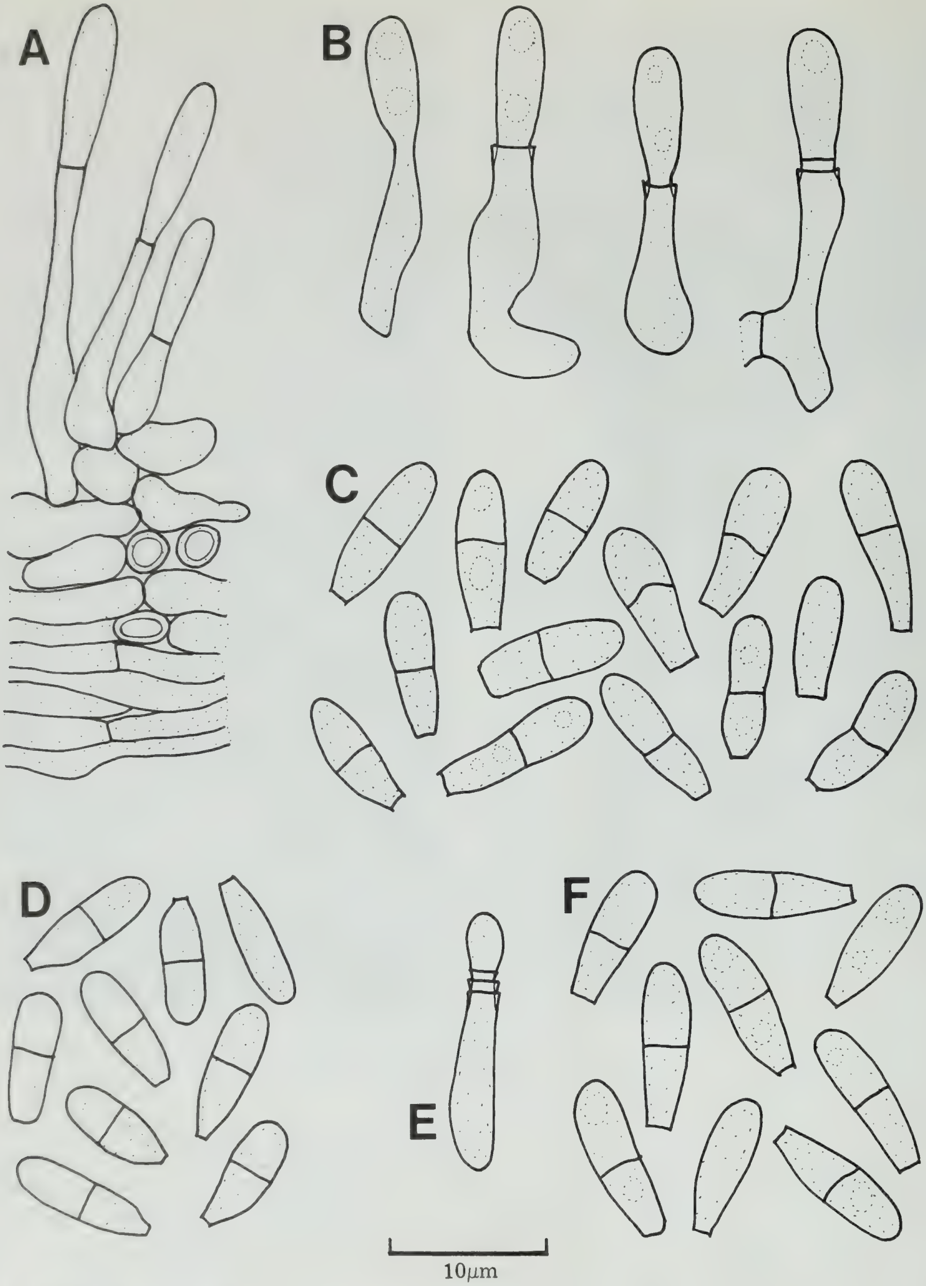

Fig. 6 *Epicladonia sandstedei.* **A–C** (IMI 240228); **A,** vertical section of pycnidial wall; **B,** conidiogenous cells; **C,** conidia. **D** (*Krypt. Exs. Vindob.* no. 1330*b*, K), conidia. **E–F** (1893, *Harmand,* Angers); **E,** conidiogenous cell; **F,** conidia.

C. cornuta (L.) Hoffm., *C. cyanipes* (Sommerf.) Vainio, *C. deformis* (L.) Hoffm., *C. fimbriata* (L.) Fr. (incl. *C. major* (Hagen) Sandst.), *C. grayi* G. K. Merrill ex Sandst., *C. ochrochlora* Flörke, *C. pleurota* (Flörke) Schaerer, *C. pyxidata* (L.) Hoffm., *C. subulata* (L.) Wigg., and *C. turgida* Ehrh. ex Hoffm.

His report from *C. caespitica* is probably an error for *C. glauca* Flörke (see below), and at least one on *C. pyxidata* probably refers to *C. merochlorophaea* Asah. (see below); some

other reports may also be due to mis-identified hosts or lichenicolous fungi. However, in addition, the fungus occurs also on at least *C. conoidea* Ahti (see below).

Distribution: Evidently widespread in Europe. Reliably reported from at least the British Isles (England), France, Germany, Sweden and Switzerland.

Observations: This fungus is easily distinguished from the other two species referred to the genus here on the basis of the predominantly 1-septate conidia.

The original material studied by Zopf could not be located in B (B. Hein, *in litt.*) but specimens from the type locality were distributed as *Krypt. Exs. Vindob.* no. 1330[a] (on *Cladonia glauca* Flörke*; B!, H!, K!). Specimens on *C.* cf. *merochlorophaea* Asah., collected by Sandstede, were also issued as no. 1330*b**. No copy of 1330[*a*] seen had good material of the fungus, but as this exsiccatum would be ideal for neotypification, and the possibility that another copy with it well-developed exists, no neotypification is proposed here. The fungus on no. 1330*b*, however, conforms to the usual concept of *Diplodina sandstedei* and so there is little doubt as to the correct application of the epithet.

Diplodina claudelii is not present amongst the remnants of Vouaux's herbarium (Rondon, 1970), nor could it be found in Claudel and Harmand's material in Angers (M. Guerlesquin, *in litt.*). This name was based on a fungus on the squamules of an unidentified *Cladonia* with pycnidia 90–150 μm diam, branched conidiophores with terminal conidia, conidiogenous cells 14–20 × 3 μm and 1-septate conidia truncated at the base and rounded at the apex which measured 10–13 × 3–3·5 μm. There is consequently little doubt that this fungus should be placed here. The absence of galls does not preclude this possibility as these are not formed in early stages of infection; pycnidia in galls and directly on podetia can occur in the same collection (e.g. IMI 240228). As 1-septate conidia were reported, it is unlikely that Vouaux was dealing with *Epicladonia stenospora* but that possibility cannot be entirely excluded as 2-guttulate conidia may appear septate if not studied carefully.

I have not seen conidia over 11·5 μm in *E. sandstedei,* but Zopf (*loc. cit.*) originally gave them as 9–14 × 3·5–4 μm.

Keissler (1930 : 571) placed *Diplodina peltigerae* as a synonym of *D. sandstedei,* perhaps because of the similar conidial dimensions, but in the absence of material of the former and the disparate hosts such a treatment cannot be accepted here (see p. 76).

Specimens: **British Isles:** England, W. Sussex, Pagham Harbour Nature Reserve, on *Cladonia conoidea* on soil amongst shingle, 30 August 1972, *B. J. Coppins* (IMI 240228!). —**France:** Docelles, on *C. chlorophaea s. lat.*, 1893, *J. Harmand* (Angers!). —**Germany:** See under Exsiccatae.

2. Epicladonia simplex D. Hawksw. **sp. nov.**
(Figs. 7A–B, 8A–B)

Similis *Epicladonia stenospora* (Harmand) D. Hawksw. sed differt in pycnidiis erumpescentibus vel superficialbus, 100–175 μm diam, et conidiis semper simpliciibus, 8·5–11(–12) × 2·5–3(–3·5) μm.

Typus: Finlandia,? Lapponia, in *Cladoniae bacilliformes* (Nyl.) Dalla Torre & Sarnth., *c.* 1925, *V. Kujala* (H—holotypus!).

Conidiomata pycnidial, usually on galls formed on squamules or podetia of the host, galls convex, tuberculate, to *c.* 1 mm diam; pycnidia immersed at first but erumpent and almost superficial at maturity, arising singly, not aggregated into stromata, scattered, dark brown, subglobose to cupuliform, 100–175 μm diam; ostiole clearly delimited, depressed, gaping to reveal the subhyaline conidia inside and so appearing whitish centrally; pycnidial wall subhyaline in the parts sunken into the galls, but brown to dark brown in the exposed parts, mainly 10–15 μm thick, composed of densely interwoven short-celled moderately thick-walled hyphae mainly 2·5–3·5 μm wide, textura intricata, but becoming almost cellular in parts. *Conidiogenous cells* holoblastic, arising from the pycnidial wall, subcylindrical

*Det. T. Ahti; the original host and material in no. 1330[*a*] was erroneously named as *C. caespiticia* (Pers.) Flörke, and in no. 1330*b* as *C. pyxidata* (L.) Hoffm., by Sandstede.

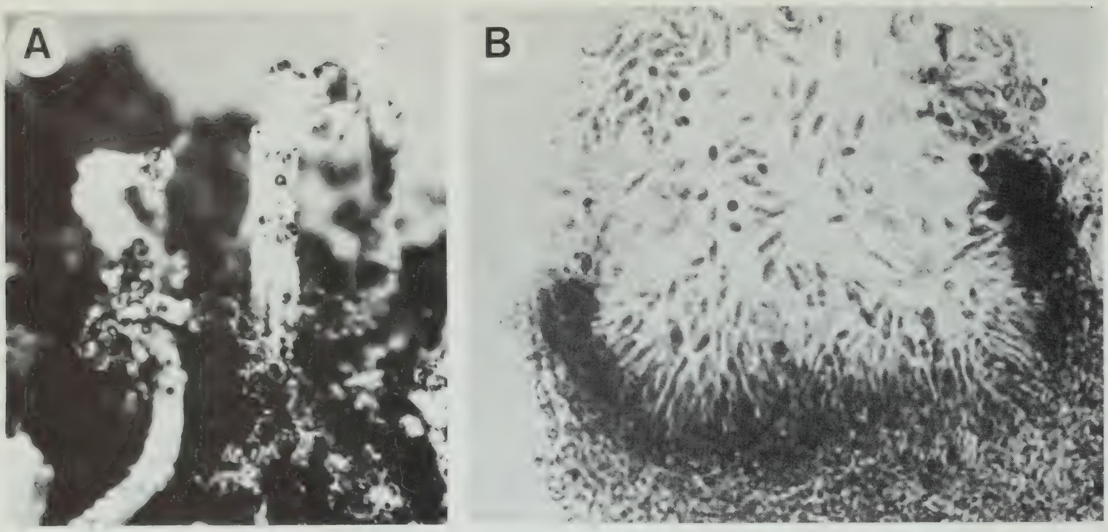

Fig. 7 *Epicladonia simplex* (H—holotype). **A,** Infected podetia showing pycnidia arising from galls and directly on the podetia (× 12·5). **B,** Vertical section of pycnidium (× 500).

to elongate ampulliform, only slightly tapered towards the apex, annellate with to 3 annellations, hyaline, smooth-walled, 7–15 × 2·5–3·5 μm. *Conidia* arising singly, not catenate, subcylindrical, always rounded at the apex, truncated at the base with a scar *c.* 1·5–2 μm wide, always simple, 2 or more guttulate, thin-walled, smooth-walled, 8·5–11(–12) × 2·5–3(–3·5) μm.

Host: Cladonia bacilliformis, usually forming galls on both the primary squamules and podetia of the host. Probably parasymbiotic.

Distribution: Finland. Known only from the original collection.

Observations: This species is most similar to *Epicladonia stenospora* (see below) from which it is distinguished by the generally larger and erumpent to almost superficial pycnidia, the more extensively pigmented and more cellular appearance of the pycnidial wall, the shape of the conidia, and further in giving rise to the formation of galls, although these are not formed immediately (Fig. 7A).

The annellations on the conidiogenous cells are more distinct in this species than in *E. sandstedei* and none were noted in *E. stenospora.* Indeed, one might interpret the conidiogenous cells of *E. simplex* as proliferating phialides rather than annellides. However, I am sceptical as to the merits of such characters at the genus level (see p. 4) and so place this species here.

3. **Epicladonia stenospora** (Harmand) D. Hawksw. **comb. nov.**
(Figs. 5C, 9A–B)

Aposphaeria stenospora Harmand, *Lich. Fr.* **3** : 308 (1907).

Conidiomata pycnidial, immersed in squamules, not associated with galls, arising singly, not aggregated into stromata, scattered, the ostiole slightly erumpent or depressed, brown, subglobose, 75–120 μm diam; ostiole clearly delimited at first but later tending to gape; pycnidial wall hyaline except in the vicinity of the ostiole where it is olivaceous brown to dark brown, mainly 7–15 μm thick but to 25 μm thick near the ostiole, wall mainly composed of densely interwoven hyphae mainly 2–3 μm wide, textura intricata but becoming almost cellular in the vicinity of the ostiole and there 4–6 μm diam. *Conidiogenous cells* holoblastic, arising from the pycnidial wall, elongate-ampulliform,

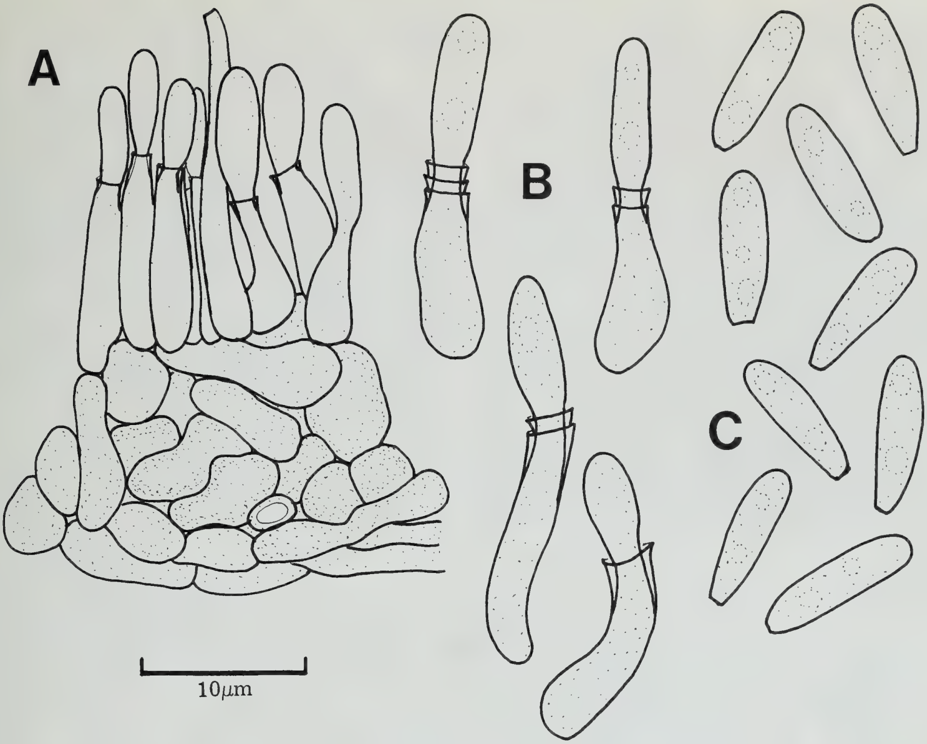

Fig. 8 *Epicladonia simplex* (H—holotype). **A,** Vertical section of pycnidial wall. **B,** Conidiogenous cells. **C,** Conidia.

strongly tapered towards the apex, hyaline, smooth-walled, no annellations seen, mainly 7–12 × 3–3·5 μm. *Conidia* arising singly, not catenate, subcylindrical to almost cymbiform, often rather irregular in shape, the apex rounded to slightly attenuated and the base narrowed and abruptly truncated by a scar *c.* 1–1·5 μm wide, simple or exceptionally 1-septate, frequently 2 or more guttulate, thin-walled, smooth-walled, 7·5–11 × 3–3·5 μm.

Hosts: Cladonia cf. *coniocraea* auct. and *C. pyxidata* (L.) Hoffm. [?] (see below). Occurring on the primary squamules in the specimen from Austria examined; no gall-like deformations are produced, but the infected tissue eventually becomes decolourized to give circular pale brownish necrotic infection spots on the host squamules (Fig. 5C). Probably parasitic.

Distribution: Austria and France.

Observations: Despite the lack of annellations this fungus is referred to *Epicladonia* in view of the very similar structure of the pycnidia and the occasional presence of 1-septate conidia. Further, the presence of distinct annellations in *E. simplex* which consistently has simple conidia and further forms galls on *Cladonia* adds weight to this taxonomy. The separation of *E. stenospora* from *E. simplex* is discussed under the latter species (p. 20).

In the original description of *Aposphaeria stenospora*, the host was named as *Cladonia pyxidata* but no locality details were provided. The original material could not be located in Angers (M. Guerlesquin, *in litt.*), but as the conidia were described as 8–9 × 2–2·5 μm it is probable that the name referred to a fungus such as that of Döbbeler's (see below), on which the above description is based. The Austrian specimen is not designated as a neotype for Harmand's name as it is rather sparse.

Specimen: **Austria:** Tirol, Hänge unmittelbar östlich des Achensees in der Nähe des Achenseehofes, on *Cladonia* cf. *coniocraea*, 13 October 1976, *P. Döbbeler* 1827 (GZU!).

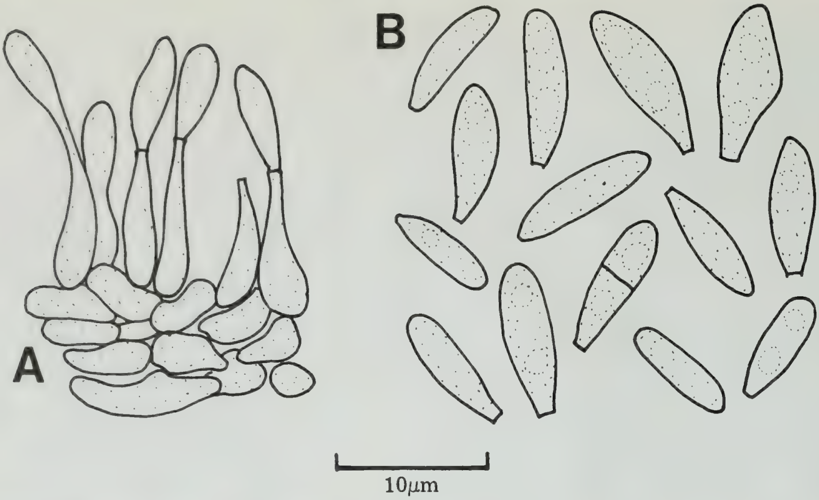

Fig. 9 *Epicladonia stenospora* (*Döbbeler 1827*). **A,** Vertical section of pycnidial wall with conidiogenous cells. **B,** Conidia.

VI. KARSTENIOMYCES D. Hawksw.

Trans. Br. mycol. Soc. **74** : 371 (1980).

Conidiomata pycnidial, arising singly, scattered or loosely aggregated, subglobose, superficial, nectrioid, translucent pale orange to deep red, ostiole irregular and forming schizogenously; walls thick, composed of thick-walled pseudosclerenchymatous cells with much-reduced lumina. *Conidiophores* cylindrical, sympodially branched. *Conidiogenous cells* holoblastic, arising acrogenously or pleurogenously, cylindrical, hyaline. *Conidia* probably dry, elongate-ellipsoid, the apex rounded and the base slightly to clearly truncate, hyaline, 1-septate, smooth-walled, guttulate.

Type species: Karsteniomyces peltigerae (P. Karsten) D. Hawksw. (syn. *Stagonopsis peltigerae* P. Karsten).

Number of species: Monotypic.

Observations: This genus appears to occupy an isolated position in the Sphaeropsidales and is unlikely to be confused with any other. *Stagonopsis* Sacc. (type species *S. pallida* (Berk. & M. A. Curtis) Sacc.) is of somewhat uncertain application, but as the type species was described as forming arcuate 7–8 septate conidia, it is most unlikely that it has anything to do with *Karsteniomyces.*

This new genus is named in honour of Petter A. Karsten (1834–1917) who made very substantial contributions to our knowledge of microfungi in Finland, including the discovery of several previously unrecognized lichenicolous species.

1. **Karsteniomyces peltigerae** (P. Karsten) D. Hawksw., *Trans. Br. mycol. Soc.* **74** : 371 (1980).
(Figs. 10A–D, 11A–E)

Stagonopsis peltigerae P. Karsten, *Meddel. Soc. Fauna Flora fenn.* **14** : 106 (1887).
Type: Finland, Tavastia australis, Tammela, Mustiala, on *Peltigera rufescens,* July 1868, *H. A. Kullhem* (H-KARST 2041—holotype!).

Conidiomata pycnidial, almost entirely superficial with only the base entering the host tissues, arising singly but often numerous and sometimes crowded together, globose, translucent pale orange at first, becoming a dark orange red with age especially around

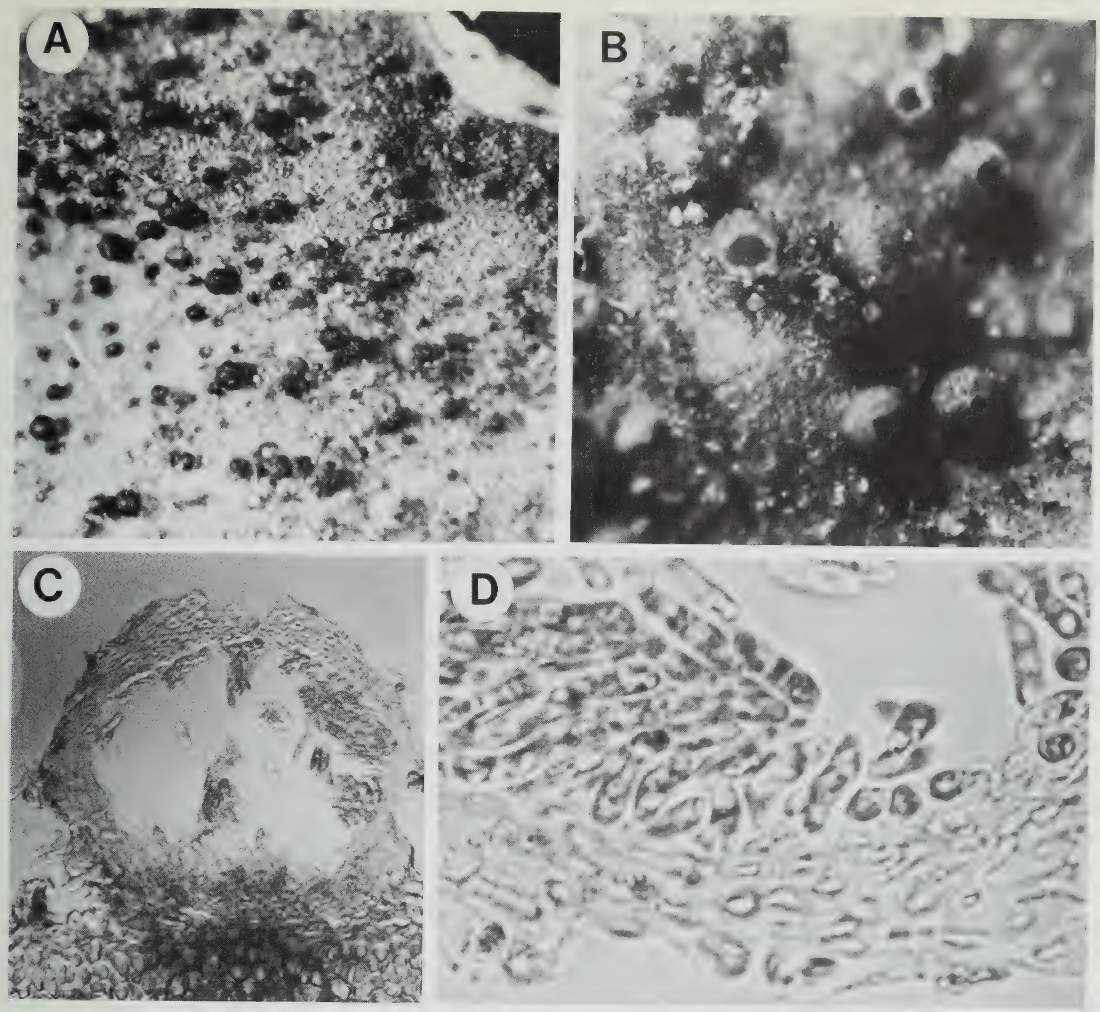

Fig. 10 *Karsteniomyces peltigerae* (H-KARST 2041—holotype). **A,** Pycnidia on the host thallus (× 25). **B,** As A showing the wide ostioles (× 50). **C,** Vertical section of pycnidium (× 250). **D,** Vertical section of pycnidial wall showing the thick-walled almost sclerenchymatous cells (× 1020).

the ostiole, mainly 75–200 μm diam but exceptionally larger, appearing nectriaceous, opening by an irregular schizogenously formed ostiole; pycnidial wall very variable in thickness, mainly 20–50 μm thick, composed of two layers, the outer comprising ± hyaline very thick-walled pseudosclerenchymatous cells with extremely narrow compressed lumina, the outer layer sometimes almost absent, very uneven externally, 5–20 μm thick, the inner layer also pseudosclerenchymatous but formed of cells with larger lumina and pigmented pale orange, 10–25 μm thick. *Conidiophores* arising from the inner walls of the pycnidial cavity, cylindrical, irregularly sympodially branched, hyaline, smooth-walled, 5–15 μm tall and 2–3(-4) μm wide. *Conidiogenous cells* arising terminally and laterally from the conidiophores, indistinguishable from the conidiophores except in the absence of septa. *Conidia* holoblastic, abundant, dry or at least not adhering, elongate-ellipsoid, the apex rounded and the base slightly to clearly truncate, hyaline, 1-septate when mature, the septum thin and sometimes undulate, 1–4 guttulate, smooth-walled, (12–)15–22(–24) × 3·5–5(–6) μm.

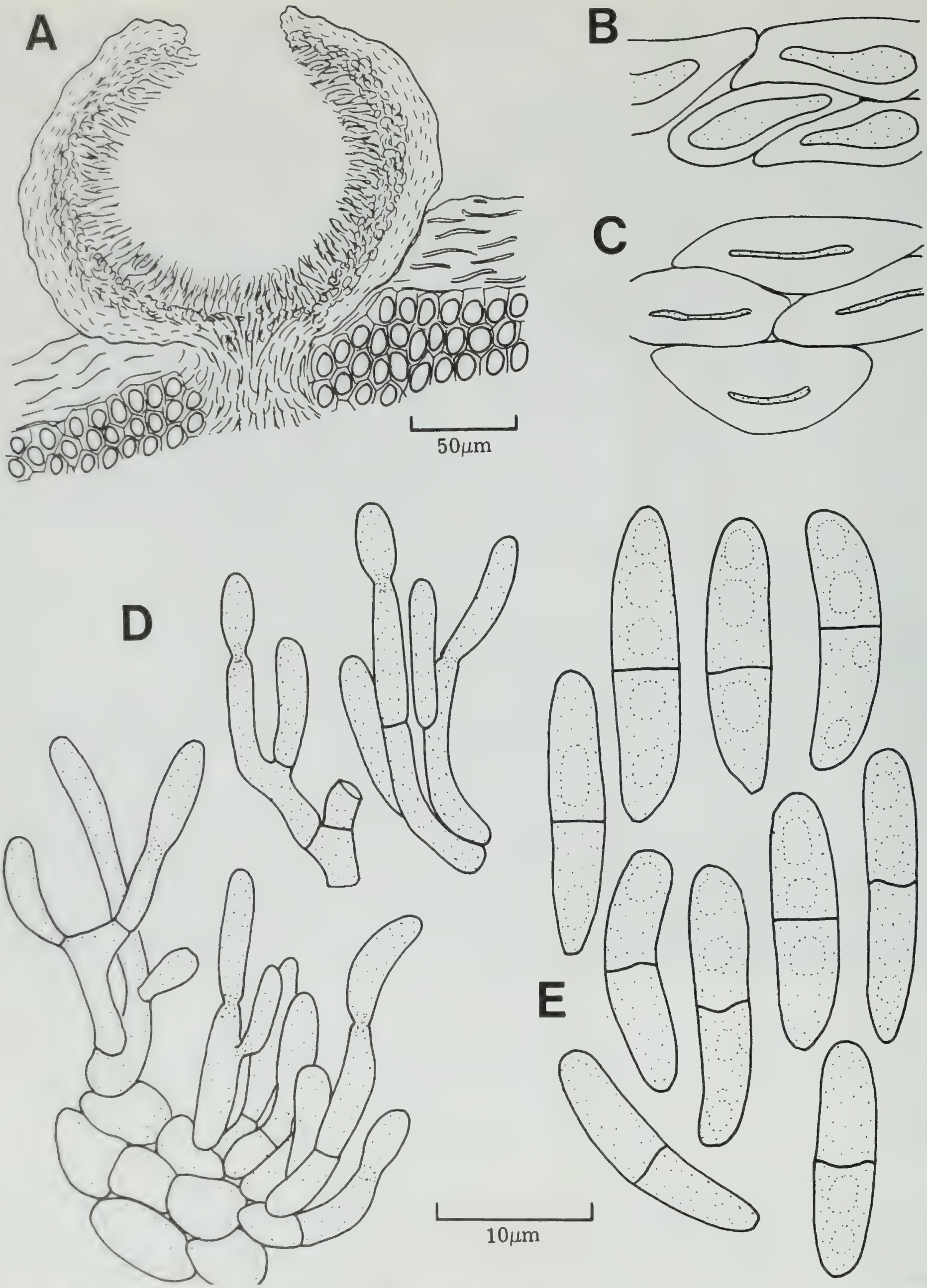

Fig. 11 *Karsteniomyces peltigerae* (H-KARST 2041—holotype). **A**, Vertical section of pycnidium. **B**, Cells from the inner part of the pycnidial wall. **C**, Cells from the outer part of the pycnidial wall. **D**, Conidiophores and conidiogenous cells. **E**, Conidia.

Host: Peltigera canina (L.) Willd. and *P. rufescens* (Weis) Humb., thalli. The type specimen was originally stated to be on *P. canina* but that host has been redetermined by Mr O. Vitikainen as *P. rufescens*. The species is, however, correctly reported here from *P. canina* (see Additional specimens). The infected thalli do not appear to be very significantly damaged by *Karsteniomyces peltigerae* and no clearly demarcated decolourized patches are produced.

Distribution: Finland and Norway. Keissler (1930 : 585) mentions two dubious records from Germany and Italy but these are in need of confirmation.

Observations: The conidia have been described as becoming up to 4-septate (Keissler, 1930 : 585) but I have only seen 1-septate conidia. I strongly suspect that reports of additional septa are due to misinterpretations of the guttules, which are often conspicuous.

Additional specimens: **Finland:** Regio aboënsis, Kakskerta Kokkila, on *Peltigera canina* and *P. rufescens*, 4 August 1934, *L. E. Kari* (H—two packets!). —**Norway:** Akershus, Oslo (Christiania), Disen, on *P. canina*, 25 March 1869, *N. G. Moe* 145 (UPS!).

VII. **KEISSLERIOMYCES** D. Hawksw. **gen. nov.**

Genus lichenicola ad Coelomycetes Sphaeropsidales pertinens. Conidomata singularia, uniloculata, dispersa, subglobosa, immersa, nigra, ostiolata, cum muris tenuibus et textura angulari compressis. Conidiophora desunt. Cellulae conidiogenae enteroblasticae, subglobosae vel breve ampulliformes, polyphialidicae, hyalinae. Conidia probaliter sicca, late fusiformia, basi leviter arcuata, hyalina, 3-septata, laevia.

Conidiomata pycnidial arising singly, scattered, subglobose, immersed, black, ostiolate; walls thin, composed of radially compressed polyhedral dark brown cells, textura angularis. *Conidiophores* absent. *Conidiogenous cells* enteroblastic, subglobose or short-ampulliform, polyphialidic, each giving rise to up to 3 conidia, hyaline. *Conidia* probably dry, broadly fusiform, the base weakly curved, hyaline, 3-septate, smooth-walled.

Type species: Keissleriomyces sandstedeanus (Keissler) D. Hawksw. (syn. *Stagonospora sandstedeana* Keissler—holotypus).

Number of species: Monotypic.

Observations: The genus *Stagonospora* (Sacc.) Sacc. nom. cons. (type species *S. paludosa* (Sacc. & Speg.) Sacc.) is characterized by conidiogenous cells forming conidia holoblastically and not polyphialides; *S. sandstedeana* consequently does not belong there. Keissler's choice of *Stagonospora* was most probably due to the rather similar conidia seen in some species of that genus. Polyphialidic conidiogenous cells are rather rare in Coelomycetes and *Keissleriomyces* has little else in common with other genera exhibiting this feature.

Although with hindsight many of Karl von Keissler's (1872–1965) taxonomic decisions amongst the lichenicolous fungi prove to be unsatisfactory, his compendium of the central European species (Keissler, 1930) remains an essential reference work to all students of lichenicolous fungi today; it is in recognition of this debt to him that the new generic name *Keissleriomyces* has been introduced here.

1. **Keissleriomyces sandstedeanus** (Keissler) D. Hawksw. **comb. nov.** (Figs. 12, 13A–E)

Stagonospora sandstedeana, Keissler, *Annln naturhist. Mus. Wein* **38** : 166 (1925).
Type: Czechoslovakia (Bohemia), Riesengebirge, Schneekoppe, on *Cladonia furcata*, *O. L. A. Ohlert* (W 1921/185—holotype!).

Conidiomata pycnidial, almost entirely immersed in the host tissues, arising singly, scattered, subglobose but often radially compressed, black, 40–75(–80) μm diam, ostiolate; pycnidial wall 7–10 μm thick, composed of usually two layers of radially compressed polyhedral pseudoparenchymatous cells, cells dark brown, moderately thick-walled, 10–14 × 3–4 μm in vertical section and mainly 6–9 μm diam in surface view. *Conidiogenous cells* enteroblastic, lining the inner wall of the pycnidial cavity except near the apex, subglobose or shortly ampulliform with swollen bases, 5–8 × 5–6 μm, polyphialidic, each cell with 1–3 phialides, hyaline. *Conidia* abundant, probably dry, broadly fusiform with the base generally more attenuated and frequently weakly curved, hyaline, 3-septate when

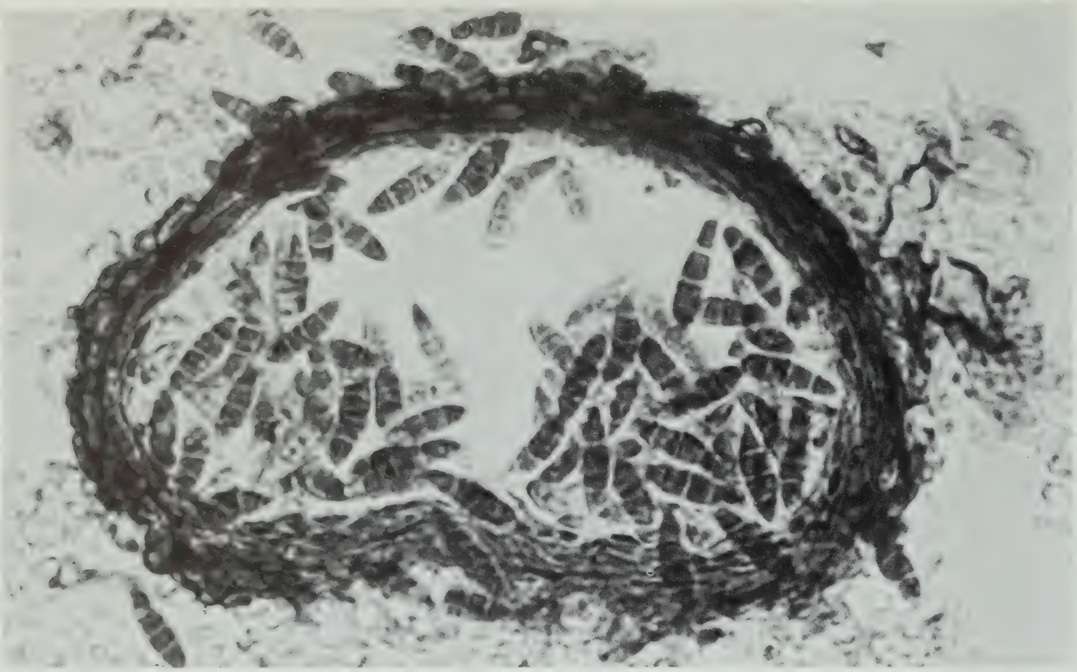

Fig. 12 *Keissleriomyces sandstedeanus* (W 1921/185—holotype), vertical section of pycnidium (× 1020).

mature, not markedly guttulate, contents rather granular, smooth-walled, 18–22 × 3·5–5 μm.

Host: Cladonia furcata (Huds.) Schrader, podetia. In the type material the pycnidia are mainly located on the upper part of the podetia, the infected part of which is slightly decolourized but not deformed. *Keissleriomyces sandstedeanus* consequently appears to be only a weak parasite or opportunist.

Distribution: Czechoslovakia. Only known from the type collection.

Observations: The characteristic polyphialides are otherwise unknown amongst the lichenicolous Coelomycetes, and no other fungus forming similar spores is recorded from any *Cladonia* species.

VIII. LAEVIOMYCES D. Hawksw. gen. nov.

Genus lichenicola ad Coelomycetes Sphaeropsidales pertinens. Conidiomata singularia, pycnidiiformia, uniloculata, dispersa, subglobosa vel irregularia, erumpescentia, nigra, cum muris plusminusve hyalinis e cellulis pseudoparenchymaticis (sed in unica textura intricatis) et ostiolis irregulariter dehiscentibus. Conidiophora desunt. Cellulae conidiogenae holoblasticae, acrogenae, subcylindrices vel elongato-ampulliformes, prolifericae, annellatae, fuscae vel brunneae, laeves. Conidia subglobosa ad ellipsoidea, basi truncata, pallide brunnea, simplicia, laevia.

Conidiomata pycnidial, arising singly, uniloculate, scattered, subglobose or irregular with somewhat convoluted internal walls, erumpent, black; walls composed of several layers of irregularly polyhedral to subglobose ± hyaline cells forming a textura angularis (but in one species reduced and hyphal, textura intricata); ostiole irregular in shape and gaping in age. *Conidiophores* absent. *Conidiogenous cells* holoblastic, lining the inner wall of the pycnidial cavity, acrogenous, subcylindrical to elongate-ampulliform, proliferating, annellate, fuscous brown to brown, smooth-walled. *Conidia* subglobose to ellipsoid, abruptly truncated at the base, a small basal frill sometimes discernible, not catenate, brown, simple, smooth-walled.

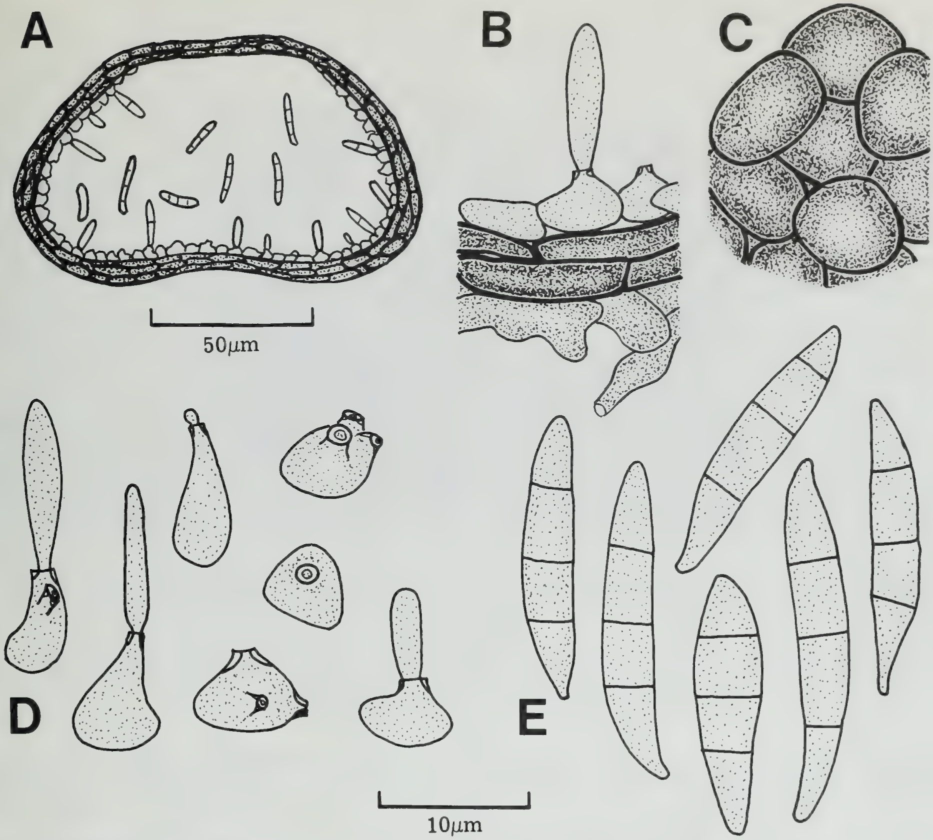

Fig. 13 *Keissleriomyces sandstedeanus* (W 1921/185—holotype). **A,** Vertical section of pycnidium. **B,** Vertical section of pycnidium wall. **C,** Surface view of pycnidial wall. **D,** Conidiogenous cells. **E,** Conidia.

Type species: Laeviomyces pertusariicola (Nyl.) D. Hawksw. (syn. *Spilomium pertusariicola* Nyl.—holotypus).

Number of species: Two, both lichenicolous.

Observations: The type species of this genus was retained in *Lichenoconium* as an interim measure by Hawksworth (1977) because a suitable generic name was considered to possibly exist amongst the non-lichenicolous Coelomycetes. Subsequent studies have failed to reveal any suitable generic name and so the genus *Laeviomyces* is introduced here to accommodate it. The generic name recalls the smooth-walled conidia (× 8000), but *L. pertusariicola* further differs from *Lichenoconium* in the massive pycnidia, hyaline and relatively flaccid pycnidial wall, the consistently brown and smooth-walled conidiogenous cells, and individually much less strongly pigmented conidia, sometimes with a recognizable basal frill.

Farr *et al.* (1979 : 1649) listed *Spilomium pertusariicola* Nyl. as the type species of *Spilomium* Nyl. However, they give the place of publication of the latter as Nylander (1858 : 91) when in fact the genus must be considered as already validly published earlier by Nylander (1856 : 337), who made no mention of *S. pertusariicola* although referring three other species to *Spilomium*. Nylander's generic name is correctly interpreted as a superfluous name for the hyphomycete genus *Sclerococcum* Fr. ex Fr., as already pointed out by Hawksworth (1975*a* : 222).

Laeviomyces could be viewed as a counterpart of *Lichenodiplis* with simple as opposed to 1-septate conidia. In view of the more complex wall structure of *Laeviomyces pertusariicola*,

Fig. 14 *Laeviomyces opegraphae* (E—holotype), vertical section of *Opegrapha niveoatra* lirellum with the hymenium partly replaced by a pycnidium of the *Laeviomyces* (× 500).

and the emphasis placed on spore septation in traditional coelomycete systematics, it seems preferrable to retain two genera while intermediate taxa are unknown.

Key to the species

1 Pycnidia 40–60 μm wide; pycnidial wall poorly developed and hyphal; conidia olivaceous brown, 3–4·5 × 1·5–2 μm . . . . **Laeviomyces opegraphae** (p. 28)

– Pycnidia 100–250(–325) μm diam; pycnidial wall well developed and pseudoparenchymatous; conidia reddish brown, 3·5–6 × 2·5–3·5 μm . **Laeviomyces pertusariicola** (p. 29)

1. Laeviomyces opegraphae D. Hawksw. sp. nov.

(Figs. 14, 15A–B)

Similis *Laeviomycei pertusariicola* (Nyl.) D. Hawksw. sed differt in pycnidiis 40–60 μm latis, muris rudimentalibus e textura intricata, et conidiis olivaceo-brunneis, 3–4·5 × 1·5–2 μm.

Typus: Magna Britannica, Scotia, Dumbarton, Loch Lomond, Gartocharn, Claddochside, in thallo *Opegraphae niveoatrae* (Borrer) Laundon, 3.iii.1980, *B. J. Coppins* 4675 (E—holotypus!).

Conidiomata pycnidial, immersed in the thallus or lirellae of the host, arising singly, scattered, sometimes becoming confluent in heavy infections, brown, 40–60 μm wide, to 100 μm tall when in lirellae, at first globose but becoming very irregular in shape, ostiole forming by an irregular breakdown of the upper wall of the pycnidium, becoming gaping and the pycnidia sometimes almost cupuliform or melanconiaceous with age; pycnidial wall poorly delimited, composed of 2–3 layers of intertwined short-celled hyphae forming a layer only 3–5 μm thick, hyphae olivaceous, sometimes becoming almost cellular just below the conidiogenous cells, subhyaline to pale olivaceous brown, 1·5–2·5 μm thick. *Conidiogenous cells* holoblastic, acrogenous, subcylindrical, proliferating, distinctly annellate with to 6 annellations, olivaceous brown, smooth-walled, 4–7(–9) × 1·5–2·5 μm. *Conidia* dry, ellipsoid, narrowed to an abruptly truncated base, basal frill sometimes visible, olivaceous brown, simple, not conspicuously guttulate, smooth-walled, 3–4·5 × 1·5–2 μm.

Host: Opegrapha niveoatra (Borrer) Laundon, thallus and hymenium of the lirellae. When on the thallus little damage occurs, but when the lirellae become infected almost the whole of the hymenium may eventually be occupied by the fungus (Fig. 14), thus precluding the possibility of ascospore formation.

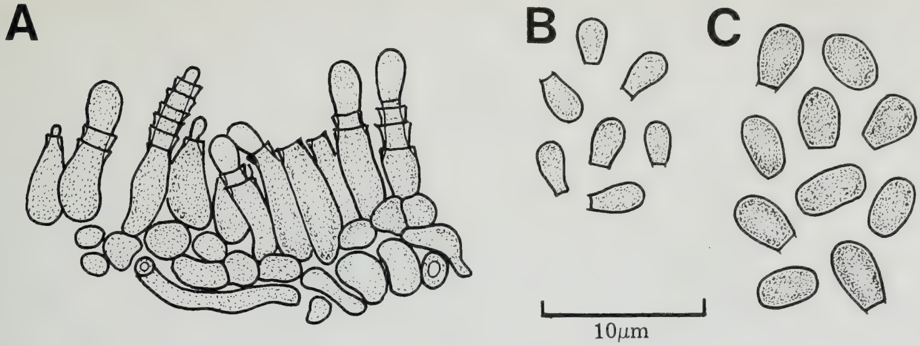

Fig. 15A–B, *Laeviomyces opegraphae* (E—holotype); **A,** conidiogenous cells; **B,** conidia. **C,** *L. pertusariicola* (IMI 186240), conidia.

Distribution: British Isles (Scotland). Evidently not uncommon in Scotland on this host and to be expected throughout the range of the host lichen.

Observations: This new species is included within *Laeviomyces* with some hesitation as the pycnidial wall is so poorly developed and almost hyphal, rather than pseudoparenchymatous as in *L. pertusariicola.* However, the pigmented and annellate conidiogenous cells and shape of the conidia are so similar in these two fungi that it seems more appropriate to view *L. opegraphae* as a species in which the wall has been reduced. It would not be prudent to describe a new genus based only on this single feature in our present state of knowledge of the lichenicolous Coelomycetes.

Additional specimens: **British Isles:** Scotland, Midlothian, Dalkeith Oak Wood, on *Opegrapha niveoatra* on *Acer,* 25 February 1977, *B. J. Coppins & C. Pope* 4696 (E!); Peebles, Dawyck Arboretum, on *O.* cf. *niveoatra* on *A. pseudoplatanus,* 10 May 1980, *B. J. Coppins* 4860 (E!).

2. Laeviomyces pertusariicola (Nyl.) D. Hawksw. **comb. nov.**
(Fig. 15C)

Spilomium pertusariicola Nyl., *Mém. Soc. Imp. Sci. nat. Cherbourg* **5** : 91 (1858); as '*pertusaricola*'.
Lichenoconium pertusariicola (Nyl.) D. Hawksw., *Trans. Br. mycol. Soc.* **65** : 233 (1975).

For description, fuller illustrations, and further synonyms see Hawksworth (1975*a* : 233–234, 1977 : 182–183).

Hosts: Buellia disciformis (Fr.) Mudd, *Pertusaria leioplaca* DC. and *P. pertusa* (Weigel) Tuck., thalli. Apparently parasymbiotic, not damaging the host thalli.

Distribution: British Isles, Canada, Denmark, France, Germany and Spain. There is also an unconfirmed report from New Caledonia (Keissler, 1933 : 387).

Observations: In the Canadian collection on *Buellia disciformis,* a host now confirmed for this fungus, the conidia tend to be slightly longer (to 7·5 μm) and rather more deeply pigmented than is usual for the species; further collections on that host may show that it merits recognition as a separate taxon. *Muellerella lichenicola* (Sommerf. ex Fr.) D. Hawksw. is also present in the collection on this *Buellia* and intimately mixed with the *Laeviomyces.*

Lichenodiplis lecanorae, which can also occur on corticolous *Pertusaria* species, is easily separated from *Laeviomyces pertusariicola* by the consistently 1-septate and generally paler rather more cylindrical and longer conidia, which have an even more strongly truncated base, as well as by the much smaller pycnidia.

Specimens (additional to those listed by Hawksworth, 1975*a*, 1977): **British Isles:** Scotland, Dunbartonshire, Loch Lomond, Ross Priory, on *Pertusaria leioplaca* on *Acer,* 13 March 1980, *B. J. Coppins* 4664 (E, IMI 247022!); Wales, Breconshire, Erw Fawr, above Elan Valley, on *P.* cf. *leioplaca*

on *Quercus*, 20 October 1979, *F. Rose* (IMI 244540!). —**Canada:** Nova Scotia, Halifax, South Park, on *Buellia disciformis* on *Acer*, April 1979, *H. J. M. Bowen* (E, IMI 244538!).

IX. LIBERTIELLA Speg. & Roum.

in Spegazzini, *Revue mycol.* **2** : 22 (1880).
Nicholsoniella Kuntze, *Rev. Gen. Pl.* **2** : 862 (1891).
Shecutia Nieuwl., *Am. Midl. Nat.* **4** : 379 (1916).

Conidiomata pycnidial, arising singly or in small groups, often aggregated, subglobose, superficial, whitish to pale orange, ostiole forming by a disintegration of the upper wall within an area delimited by a reddish-brown ring of tissue; walls composed of almost hyaline very thick-walled pseudoparenchymatous cells, often interspersed with orange granules. *Conidiophores* hyaline, irregularly sympodially branched, short, cylindrical. *Conidiogenous cells* enteroblastic, phialidic, arising laterally or terminally from the conidiophores, rarely proliferating. *Conidia* adhering in gelatinous masses, ellipsoid to obovoid with a slightly truncated base, hyaline, simple, smooth-walled.

Type species: Libertiella malmedyensis Speg. & Roum.

Number of species: Monotypic. Other species previously referred to this genus are now placed in different genera (see Index).

Observations: Both *Nicholsoniella* Kuntze and *Shecutia* Nieuwl. were introduced as new names for *Libertiella* in the belief that *Libertiella* was a homonym of the earlier *Libertella* Desm.; Nieuwland (1916) was evidently unaware of the new name introduced by Kuntze. However, as pointed out by Sutton (1977 : 113), in coining the new generic name *Libertiella*, Spegazzini and Roumeguère deliberately inserted the '*i*' and made it clear in a footnote that they were doing this to prevent confusion with *Libertella* Desm. The generic name *Libertiella* is consequently not to be treated as a later homonym of *Libertella* and can be retained.

1. **Libertiella malmedyensis** Speg. & Roum., *in* Spegazzini, *Revue mycol.* **2** : 22 (January 1880).
(Figs. 16A–B, 17A–E)

Type: Belgium, 'prope malmedyanum', on *Peltigera spuria* (Ach.) DC., 'Hieme', *M.-A. Libert* (BR—holotype, non vidi; K—isotype!).
Nicholsoniella malmedyensis (Speg. & Roum.) Kuntze, *Rev. Gen. Pl.* **2** : 863 (1891).
Shecutia malmedyensis (Speg. & Roum.) Nieuwl. *Am. Midl. Nat.* **4** : 379 (1916).
Zythia peltigerae Lib. ex Cooke, *Grevillea* **8** : 83 (March 1880), nom. illegit. (Art. 63).
Type: Belgium, [Malmédy], on *Peltigera spuria* (Ach.) DC., *M.-A. Libert* (BR—holotype, non vidi; K—isotype!).
Libertiella peltigerae (Lib. ex Cooke) Keissler, *Rabenh. Krypt.-Fl.* **8** : 582 (1930).

Exsiccatae: Roumeguère, *Fungi sel. Gall.* no. 671 (K!).—Thümen, *Mycoth. univ.* no. 1775 (K!).

Conidiomata pycnidial, superficial, with only the base immersed in the host, arising singly or more commonly in groups, often aggregated, subglobose, whitish to pale orange, mainly (100–)150–200(–300) μm diam, becoming flattened at the apex with the development of the ostiole; ostiole forming after the pycnidial cavity is full of spores, demarcated by a limiting reddish-brown ring of tissue about 25 μm wide encircling the whitish 50–75 μm diam pore; pycnidial wall mainly 10–12 μm thick, composed of $\pm$ hyaline translucent thick-walled pseudosclerenchymatous cells, cells mainly 3–4·5 μm thick, walls of the inner layers of cells thinner and these cells often orientated perpendicularly to the outermost layer(s) which are often interspersed with minute orange granules also present on the wall surface. *Conidiophores* arising from the inner wall of the pycnidial cavity, cylindrical, irregularly sympodially branched, hyaline, smooth-walled, 2–8 μm tall and 3–3·5 μm

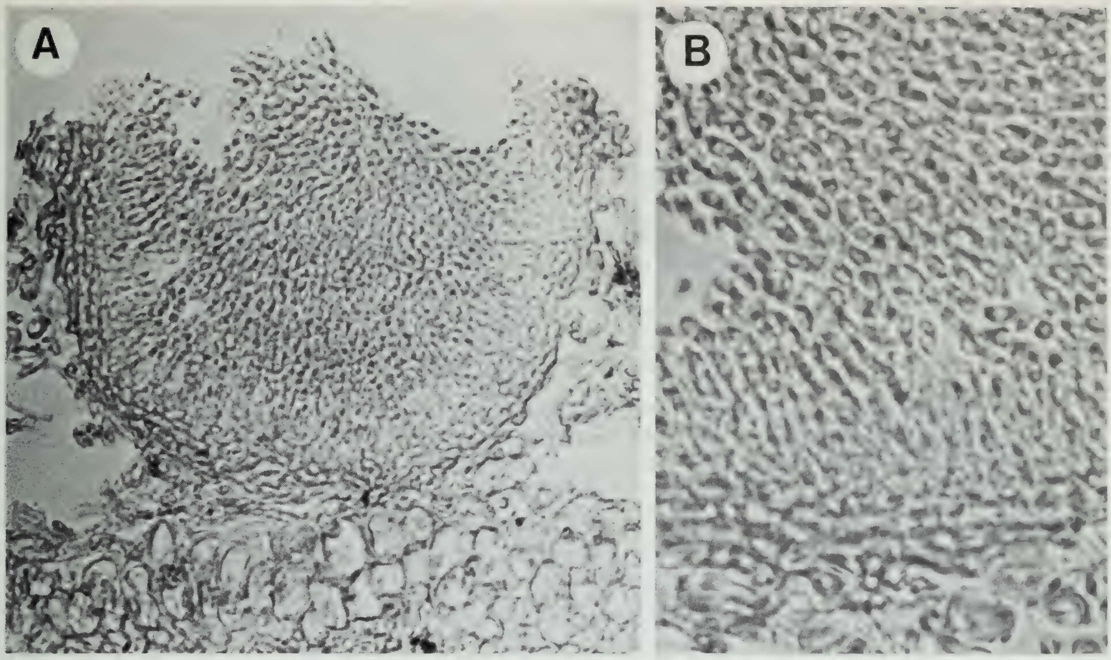

Fig. 16 *Libertiella malmeydensis* (K—isotype). **A,** Vertical section of pycnidium (× 500). **B,** Vertical section of pycnidial wall with conidiogenous cells and conidia (× 1020).

wide. *Conidiogenous cells* enteroblastic, arising terminally and laterally from short conidiophores or directly from the inner wall of the pycnidial cavity, cylindrical, phialidic with a short collarette, rarely proliferating, hyaline, 10–12 × 2–3·5 μm. *Conidia* abundant, adhering together in gelatinous masses, ellipsoid to obovoid with a slightly truncated base, rather irregular in outline, hyaline, simple, rarely guttulate, smooth-walled, (5–)6–8 × (2–)3–4 μm.

Host: Peltigera spuria (Ach.) DC., thallus. The pycnidia arise most abundantly on the underside of the thallus but are also present in groups on the upper cortex, especially where soredia were formerly produced in the *P. erumpens* (Taylor) Vainio morph of this species. *Libertiella malmedyensis* causes relatively minor damage to infected thalli and does not lead to the formation of necrotic patches. The host of this fungus has consistently been cited as *P. polydactyla* (Necker) Hoffm., but Libert's material is *P. spuria* and not *P. polydactyla.*

Distribution: Belgium and Poland. It was evidently very abundant in the type locality as in addition to sending material to several herbaria, Libert left enough in Brussels for the exsiccatae of both Roumeguère and de Thümen.

Observations: Libertiella malmedyensis shows some similarity to *Karsteniomyces peltigerae* (p. 22) but differs in both the method of conidiogenesis and the non-septate and differently shaped ascospores; in addition the pycnidial wall in *K. peltigerae* has much more thickened pseudosclerenchymatous cells than *L. malmedyensis* and the conidia are not markedly gelatinous.

Keissler (1930 : 582) took up the epithet '*peltigerae*' for this species as he believed that was published in March 1880 while '*malmedyensis*' came out in April 1880. The issue of the *Revue mycologique* including Spegazzini's paper was volume 2 part 1 as this has the title of his paper printed on the front wrapper together with 'Janvier 1880'. In *Grevillea* volume 8 number 47, dated March 1880 on the first page, and which included Cooke's article 'Relique Libertianae' on pp. 81–87, on p. 120 of this same number appears under 'Cryptogamic Literature' the entry 'ROUMEGUÈRE, C. Reliquae Libertianae, in "Revue Mycologique". Jan.,

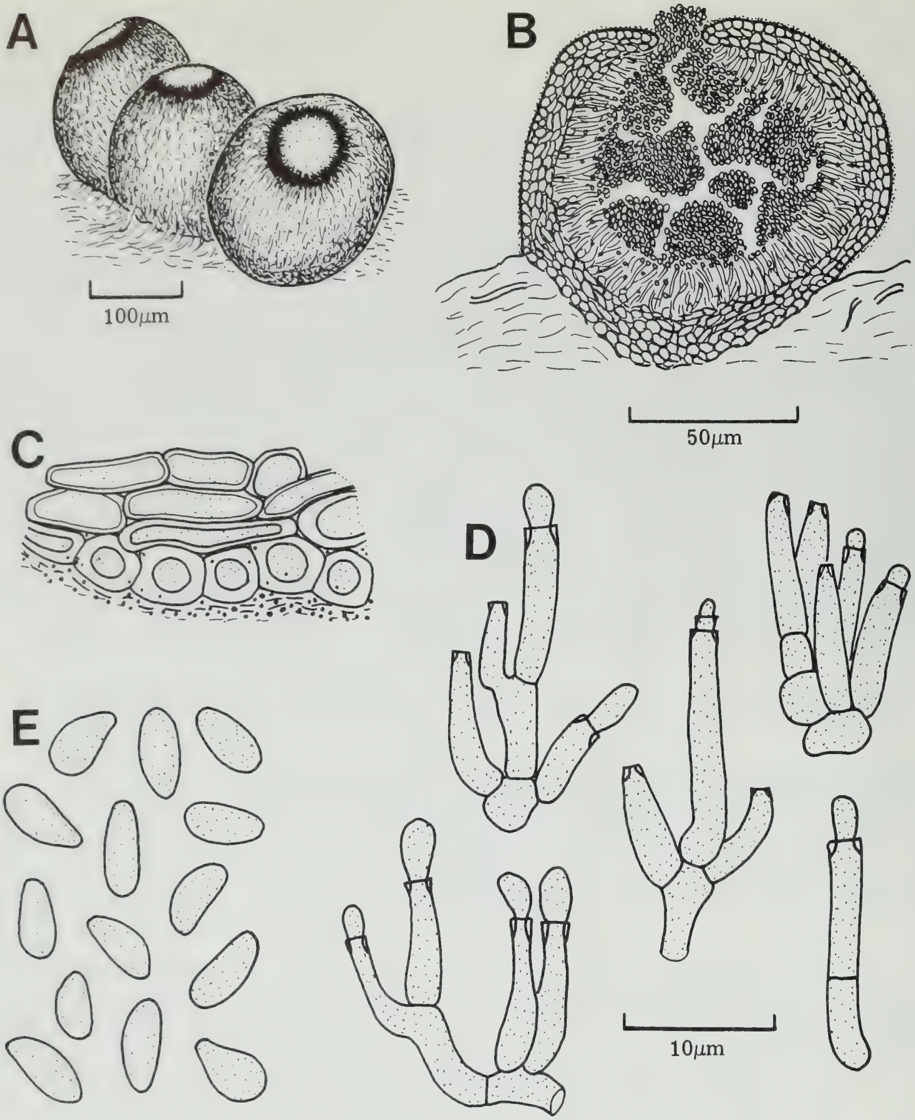

Fig. 17 *Libertiella malmeydensis* (K—isotype). **A,** Pycnidia on the host thallus showing the deeply pigmented ring around the ostiole. **B,** Vertical section of pycnidium. **C,** Vertical section of pycnidial wall with granular encrustations on the outer cells. **D,** Conidiophores and conidiogenous cells. **E,** Conidia.

1880.' There can consequently be no doubt that Spegazzini's article, which was an appendix to that of Roumeguère, appeared before the printing and distribution of the part of *Grevillea* including Cooke's paper. The epithet '*malmedyensis*' must consequently be reinstated for this species because it predates '*peltigerae*', and in the absence of evidence to the contrary '*malmedyensis*' is taken to have been validly published in January 1880. Keissler's date for '*malmedyensis*' might have arisen from a hasty confusion of the wrappers of the *Revue;* volume 2 part 2 has 'Avril 1880' printed on it.

Roumeguère's exsiccatum included a description of *Libertiella malmedyensis* on the printed label. The fascicle including no. 671, fasc. VII, was also issued in January 1880 according to a mention in *Revue mycologique* **2**(1): 27. I have not been able to sequence the

exsiccata and journal article within January 1880; it is even possible that they were distributed simultaneously to save postage as Roumeguère then edited the journal!

Additional specimen: **Poland:** Puszcza Piska, on *Peltigera spuria*, June 1958, *J. Zielińska* (K!).

X. LICHENOCONIUM Petrak & H. Sydow

Beih. Repert. Spec. nov. Regni veg. **42** : 432 (1927).

See Hawksworth (1977 : 170) and Sutton (1980 : 118) for modern descriptions of the genus.

Type species: Lichenoconium lichenicola (P. Karsten) Petrak & H. Sydow.

Number of species: Eight, all obligately lichenicolous.

Observations: Two additional species, *Lichenoconium boreale* (P. Karsten) Petrak & H. Sydow and *L. pertusariicola* (Nyl.) D. Hawksw., were only retained in *Lichenoconium* by Hawksworth (*loc. cit.*) pending further research on the generic names proposed for Coelomycetes. From the major studies of Sutton (1977, 1980) it is evident that there is no currently acceptable genus available for either of these two fungi. *L. pertusariicola* is therefore referred to the new genus *Laeviomyces* above, and its separation from *Lichenoconium* is discussed under that name (p. 27). *L. boreale* is not a lichenicolous fungus but occurs on conifer lignum; that fungus differs from *Lichenoconium* in having a pycnidial wall which consists of interwoven hyphae (textura intricata), very slender conidiogenous cells, and almost colourless to pale olivaceous conidia which are ellipsoid to almost allantoid, clearly guttulate, with smooth walls when studied by light microscopy (although with a delicate close-packed verruculose ornamentation in SEM). The new generic name *Xeroconium* D. Hawksw.* is therefore introduced for this species here; a detailed description and illustrations of *Xeroconium boreale* (under the name *Lichenoconium boreale*) were presented in Hawksworth (1977 : 171–172, fig. 1A, pl. 22 A–E) and further drawings are given by Sutton (1980 : 119, fig. 56 A–C).

Key to the species

1 Pycnidia mainly exceeding 100 μm diam 2
– Pycnidia mainly less than 80 μm diam 5

2 Conidia mainly exceeding 4 μm in length, distinctly echinulate or verruculose . . . 3
– Conidia (2–)2·5–3·5(–4) × 2–3 μm, rather smooth-walled; pycnidia (60–)80–120(–150) × 50–80(–100) μm . . . . **Lichenoconium pyxidatae** (p. 36)

3 Conidia globose to subglobose, sometimes rather angular 4
– Conidia ellipsoid with a tapering and abruptly truncated base, (4–)6–8(–9) × 3–4(–6) μm; pycnidia 100–200 μm diam; conidiogenous cells (6–)8–13(–15) × 2–3·5(–4·5) μm . . . . **Lichenoconium lichenicola** (p. 36)

4 Conidia (2·5–)3–4·5(–6) μm diam; pycnidia (80–)100–175(–200) μm diam; conidiogenous cells (5–)6–8(–11) × (2–)2·5–4 μm . . . . **Lichenoconium xanthoriae** (p. 37)
– Conidia 5–7(–7·5) × 3·5–5(–6) μm; pycnidia 100–175(–200) μm diam; conidiogenous cells (7–)8–10(–12) × (2·5–)3–3·5 μm . . . . **Lichenoconium cargillianum** (p. 35)

5 Pycnidia mainly exceeding 50 μm diam; conidia mainly exceeding 3·5 μm diam . . . 6
– Pycnidia (20–)30–50(–60) μm diam; conidiogenous cells (3·5–)4–5(–6) × (2–)3–3·5(–4) μm; conidia 2–3·5(–4) μm . . . . **Lichenoconium erodens** (p. 35)

***Xeroconium** D. Hawksw. **gen. nov.**
Genus ad Coelomycetes Sphaeropsidales pertinens. Similis generi *Lichenoconio* Petrak & H. Sydow sed differt in muris pycnidiis textura intricata, cellulis conidiogenis gracilioribus, et conidiis ellipsoideis ad plusminusve allantoideis, subhyalinis ad pallide olivaceis, gutullatis, laevibus (sed per microscopium electronicum minuto-verruculosis).—Species holotypica, adhuc unica, est **Xeroconium boreale** (P. Karsten) D. Hawksw. **comb. nov.** (basionym: *Levieuxia borealis* P. Karsten, *Hedwigia* **26** : 126, 1887).

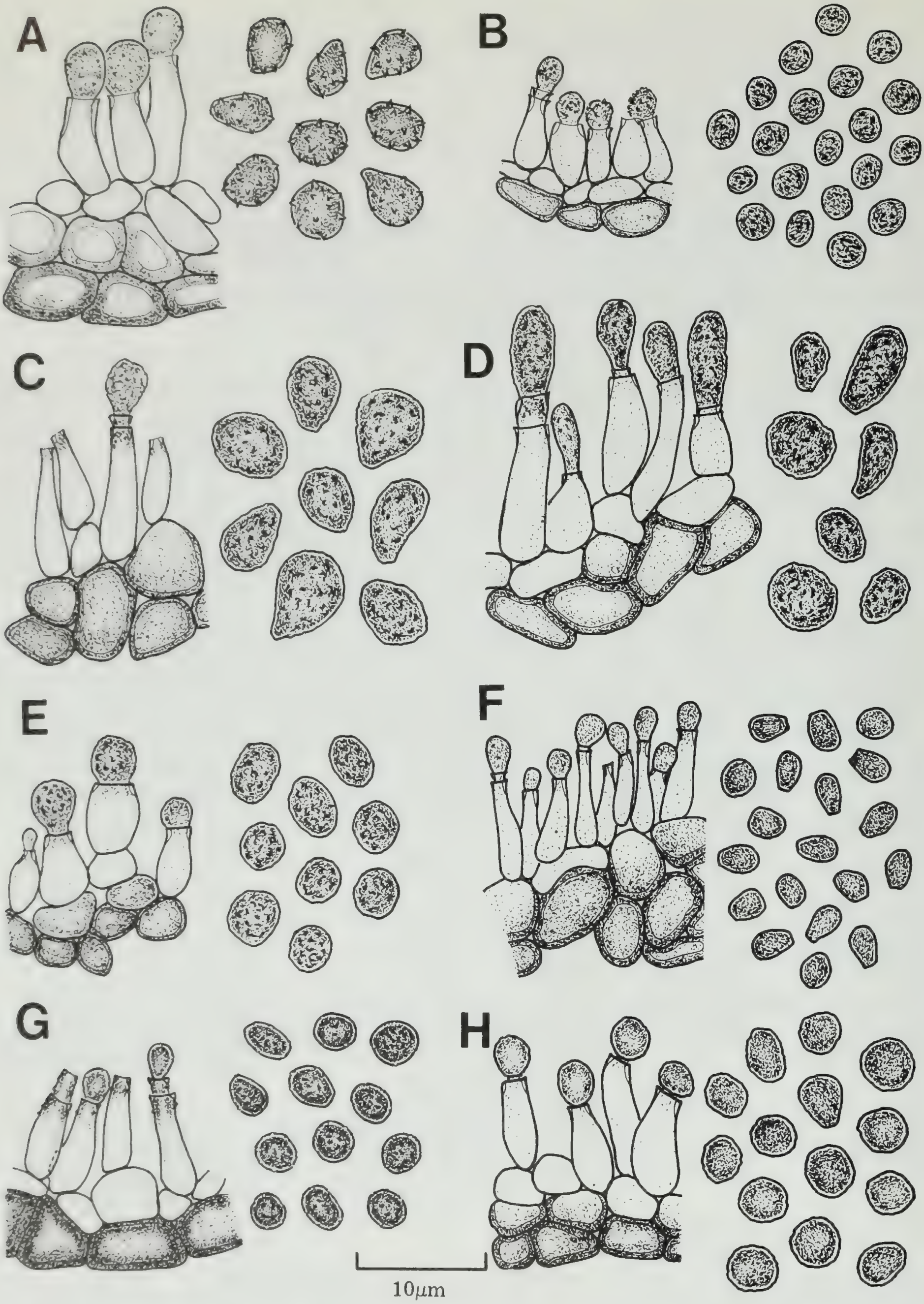

Fig. 18 *Lichenoconium* species, conidiogenous cells and conidia. **A**, *L. echinosporum* (UPS—holotype). **B**, *L. erodens* (herb. Christiansen—holotype). **C**, *L. cargillianum* (E—holotype). **D**, *L. lichenicola* (H-KARST 1246—holotype). **E**, *L. lecanorae* (IMI 192264). **F**, *L. pyxidatae* (L—holotype). **G**, *L. usneae* (K—isotype). **H**, *L. xanthoriae* (C—holotype). Reproduced from Hawksworth (1977 : 162, 164).

6 Conidiogenous cells mainly exceeding 7 μm tall 7
– Conidiogenous cells (4–)5–7(–8) × (2–)3–3·5(–4) μm; conidia (2·5–)3–4·5(–5·5) μm; pycnidia (30–)40–80(–100) μm diam . . . . . . **Lichenoconium lecanorae** (p. 36)

7 Conidia verruculose, (2·5–)3–4(–5) μm diam; pycnidia (40–)50–80(–100) μm diam; conidiogenous cells (5–)7–9(–11) × (2–)2·5–3·5(–4) μm . . **Lichenoconium usneae** (p. 37)
– Conidia sparsely echinulate, 4·5–5 × 3–4 μm; pycnidia 65–125 μm diam; conidiogenous cells (7–)8–10(–11) × 2–3 μm . . . . **Lichenoconium echinosporum** (p. 35)

1. Lichenoconium cargillianum (Lindsay) D. Hawksw., *Persoonia* **9** : 172 (1977).
(Fig. 18C)

See Hawksworth (1977 : 172–3) for description, illustrations and synonymy.

Hosts: Parmelia perforata Ach., *Ramalina yemensis* (Ach.) Nyl. and *Usnea florida* (L.) Wigg., predominantly in apothecia.

Distribution: British Isles, Mexico and New Zealand.

2. Lichenoconium echinosporum D. Hawksw., *Persoonia* **9** : 173 (1977).
(Fig. 18A)

See Hawksworth (1977 : 173–174) for description and illustrations.

Host: Heterodea muelleri (Hampe) Nyl., a pathogen on the thallus.

Distribution: Australia. I have only seen the holotype but Filson (1978 : 17) reports seeing pale brown necrotic patches like those due to this fungus from a wide range of Australian localities.

3. Lichenoconium erodens M. S. Christ. & D. Hawksw., *in* Hawksworth, *Persoonia* **9** : 174 (1977).
(Fig. 18B)

See Hawksworth (1977 : 174–177) for description and illustrations.

Hosts: Cladonia coniocraea (Flörke) Sprengel, *C. digitata* (L.) Hoffm., *Evernia prunastri* (L.) Ach., *Hypogymnia bitteriana* (Zahlbr.) Krog, *H. physodes* (L.) Nyl., *Lecanora chlarona* (Ach.) Nyl., *L. conizaeoides* Nyl. ex Crombie, *Parmelia afrorevoluta* Krog & Swinscow (syn. *P. revoluta* auct. p.p.), *P. caperata* (L.) Ach., *P. crinita* Ach., *P. galbina* Ach., *P. laevigata* (Sm.) Ach., *P. perlata* (Huds.) Ach., *P. saxatilis* (L.) Ach., *Parmeliopsis ambigua* (Wulfen) Nyl., *Pertusaria hymenea* (Ach.) Schaerer and *P. pertusa* (Weigel) Tuck.

Distribution: Austria, British Isles, Denmark, France, Germany, Sweden and the U.S.A.

Observations: A wide-ranging species which has been found on seven additional hosts since its original description (Hawksworth, 1977). By far the most pathogenic species of the genus, typically producing bleached areas on thalli which subsequently die. In cases where this and other species of the genus are able to occur on the same host species, the symptoms generally differ, *Lichenoconium erodens* always causing the most damage. This is also true for the additional hosts included in the list above, including the *Cladonia* species and *Lecanora conizaeoides;* its effects on the latter are illustrated and compared with those due to *L. lecanorae* by Christiansen (1980).

Specimens (additional to those listed in Christiansen, 1980; Hawksworth, 1977, 1980*c*; and Hawksworth & Minter, 1980): **Austria:** Steiermark, Grazer Bergland, Graz, Maria Trost, on *Hypogymnia physodes,* 24 March 1974, *J. Hafellner* 568 (GZU!); Steiermark, Frauenalm S. of Musau, on *Cladonia digitata,* 18 June 1978, *J. Hafellner* 3897 (GZU!). —**British Isles:** England, Middlesex, Ruislip, Park Wood, on *Cladonia coniocraea* on *Quercus,* 9 December 1979, *D. L. Hawksworth* 5009 (IMI 244544*a*!); S. Devon, Cornwood, Dendles Wood, on *Parmelia laevigata,* 29 February 1976, *D. L. Hawksworth* 4293b (IMI 201661*b*!); S. Devon, Okehampton, nr Fatherford Viaduct, on *Hypogymnia*

physodes on *Quercus*, 30 March 1979, *D. L. Hawksworth* 4903 (IMI 236902!); Dorset, Studland Heath, on *H. physodes* on *Betula*, 25 June 1979, *D. L. Hawksworth* 4952 (IMI 240076!); Hampshire, New Forest, Stubbs Wood, on *H. physodes*, 13 May 1979, *D. L. Hawksworth* 4936 (IMI 238699!); S. Somerset, nr Stoke Perol, on *H. physodes* on *Quercus*, 6 October 1979, *D. L. Hawksworth* 5002 (IMI 243338!); S. Somerset, Porlock, Horner Combe, on *P. laevigata* on *Betula*, 21 September 1980, *D. L. Hawksworth* 5073 (IMI 251491!); Scotland, Dunbartonshire, Loch Lomond, Ross Park, on *P. caperata* on *Quercus*, 9 October 1978, *B. J. Coppins* 3688 (E, IMI 232973!); Wales, Anglesey, Abberfraw sand dunes, on *Evernia prunastri*, 17 October 1977, *D. L. Hawksworth* 4651 (IMI 217423!).

4. Lichenoconium lecanorae (Jaap) D. Hawksw., *Bull. Br. Mus. nat. Hist.* (Bot.) **6 :** 183 (1979).
(Fig. 18E)

See Hawksworth (1977 : 178–182, sub *L. parasiticum* D. Hawksw.) for description and illustrations.

Hosts: Evernia prunastri, Lecanora admontensis Zahlbr., *L. carpinea* (L.) Vainio, *L. chlarotera* Nyl., *L. conizaeoides* Nyl. ex Crombie, *L. pallida* (Schreber) Rabenh., *L. polytropa* (Hoffm.) Rabenh., *L. subfuscata* Magnusson, *L. superfluens* Magnusson, *Parmelia borreri* (Sm.) Turner, *P. galbina* Ach., *P. pastillifera* (Harm.) R. Schub. & Klem., *P. saxatilis* (L.) Ach., *P. sulcata* Taylor, *Rhizoplaca chrysoleuca* (Sm.) Zopf and *Squamarina lentigera* (Weber) Poelt. There are also some unconfirmed literature reports (see Hawksworth 1977 : 179).

Distribution: Austria, ?Belgium, British Isles, Canada, Czechoslovakia, Denmark, France, Germany, Hungary, Italy, Netherlands, Spain, Sweden, Switzerland and the U.S.A.

Observations: The symptoms of this species on *Lecanora conizaeoides* are illustrated and compared with those due to *Lichenoconium erodens* by Christiansen (1980).

Specimens (additional to those listed by Hawksworth, 1977): **Austria:** Steiermark, Schladminger Tauren, Kleinsölk-Obertal, on *Lecanora polytropa*, 12 August 1974, *J. Hafellner* 3932 (GZU!). —**British Isles:** England, Hampshire, New Forest, Stubbs Wood, on *Parmelia sulcata*, 13 May 1979, *D. L. Hawksworth* 4937 (IMI 238700!); S. Devon, Slapton Ley Nature Reserve, Peasdish, on *P. sulcata*, 23 August 1980, *D. L. Hawksworth* 5044b (IMI 2511262!); *loc. cit.*, on *Lecanora* sp., 23 August 1980, *D. L. Hawksworth* 5044a (IMI 251261!). —**France:** Dept. Isère, Rhône-Tal E. Lyon, on *Squamarina lentigera*, 13 July 1975, *J. Hafellner* 1575 (GZU!). —**Italy:** Südtirol, Mendelgebirge, Penegal SW. von Bozen, on *Lecanora carpinea*, 20 October 1975, *J. Hafellner* 1092 (GZU!); Ötztaler Alpen, Vinschgau, on *Rhizoplaca chrysoleuca*, 18 October 1975, *J. Hafellner* 997 p.p. (GZU!).

5. Lichenoconium lichenicola (P. Karsten) Petrak & H. Sydow, *Beih. Repert. nov. Spec. Regni veg.* **42 :** 432 (1927).
(Fig. 18D)

See Hawksworth (1977 : 177–178) for description and illustrations. Further drawings are provided by Sutton (1980 : 119 fig. 55a–c).

Host: Physcia aipolia (Ehrh. ex Humb.) Fürnrohr, apothecia.

Distribution: Finland. Known only from the type collection.

6. Lichenoconium pyxidatae (Oudem.) Petrak & H. Sydow, *Beih. Repert. nov. Spec. Regni veg.* **42 :** 435 (1927).
(Fig. 18F)

See Hawksworth (1977 : 184–185) for description and illustrations.

Hosts: Cladonia arbuscula (Wallr.) Rabenh., *C. cenotea* (Ach.) Schaerer, *C. fimbriata* (L.) Fr., *C. incrassata* Flörke, *C. pocillum* (Ach.) O.-J. Rich., and *C. pyxidata* (L.) Hoffm.; usually on the podetia but occasionally on squamules. There are also unconfirmed reports from additional hosts in *Cladonia* and other genera, the latter certainly erroneous (see Hawksworth, *loc. cit.*).

Distribution: Austria, British Isles, Denmark, France, Germany, the Netherlands and Sweden.

Observations: Harmand (1907 : 226) stated that *Cladonia rangiferina* f. *moribunda* Harm. was based on deformed podetia with verrucae caused by a fungus close to *Lichenoconium pyxidatae* but 'il se distingue par des spores franchement brunes et ovoïdes' according to Vouaux who Harmand indicates studied the material. I have not seen type or authentic material of this taxon.

7. Lichenoconium usneae (Anzi) D. Hawksw., *Persoonia* **9 :** 185 (1977).
(Fig. 18G)

See Hawksworth (1977 : 185–190) for description, illustrations and synonymy.

Hosts: Anaptychia ciliaris (L.) Körber, *Bryoria fuscescens* (Gyelnik) Brodo & D. Hawksw., *Cladonia arbuscula* (Wallr.) Rabenh., *C. cariosa* (Ach.) Sprengel, *Hypogymnia physodes* (L.) Nyl., *Lecanora pacifica* Tuck., *Letharia vulpina* (L.) Hue, *Parmelia conspersa* (Ehrh. ex Ach.) Sprengel, *P. exasperata* (Ach.) de Not., *P. glabratula* (Lamy) Nyl., *P. olivacea* (L.) Ach., *P. pulla* Ach., *P. rudecta* Ach., *P. saxatilis* (L.) Ach., *P. verruculifera* Nyl., *Physcia aipolia* (Ehrh. ex Humb.) Fürnrohr, *P. stellaris* (L.) Nyl., *Physconia pulverulacea* Moberg, *Ramalina* cf. *baltica* Lettau, *R. calicaris* (L.) Fr., *R. fraxinea* (L.) Ach., *R. siliquosa* (Huds.) A. L. Sm., *R. subgeniculata* Nyl., *Usnea filipendula* Stirton aggr., and *U.* cf. *florida* (L.) Wigg. For unconfirmed literature reports see Hawksworth (*loc. cit.*).

Distribution: Austria, British Isles, Canada, Canary Islands, Czechoslovakia, Denmark, France, Germany, Italy, Norway, Spain, Sweden, Switzerland, Yugoslavia (Keissler, 1933 : 388) and the U.S.A.

Specimens (additional to those listed in Hawksworth, 1977): **Austria:** Steiermark, Stubalpe, Gaberl, on *Usnea* cf. *florida,* 19 December 1976, *J. Poelt & J. Hafellner* 1825 (GZU!); Steiermark, Kreuzberg, on *Cladonia* sp., 16 March 1975, *W. Möschl & H. Pittoni* [herb. Hafellner 437] (GZU!); Nockgruppe, Afritzer Berge, Kärten, on *Usnea* sp., 27 August 1974, *J. Poelt* (GZU!). —**British Isles:** England, S. Devon, Slapton, Duck Marsh, on *Ramalina fraxinea,* 5 September 1978, *D. L. Hawksworth* 4869 (IMI 231752!); Scotland, Midlothian, Carlops, Hobbies House, on *Bryoria fuscescens,* 29 March 1977, *B. J. Coppins* 2727 (E!). —**Canada:** Alberta, Kananaskis Range, between Wind Ridge and Mount Longhead, on *Letharia vulpina,* 22 June 1978, *D. C. Lindsay* (IMI 229869*b*!). —**France:** Dept. Vas, Ile de Port Cros, on *Ramalina calicaris,* 17 July 1973, *Y. Rondon* [herb. Hafellner 1826] (GZU!).

8. Lichenoconium xanthoriae M. S. Christ., *Friesia* **5 :** 212 (1956).
(Fig. 18H)

See Hawksworth (1977 : 190–192) for description and illustrations.

Hosts: Cetraria sepincola (Ehrh.) Ach., *Cetrelia olivetorum* (Nyl.) Culb. & C. Culb. s. lat., *Xanthoria parietina* (L.) Th. Fr., *X. polycarpa* (Hoffm.) Rieber. The collections on *Cetrelia* have been reported on by Hawksworth & Minter (1980).

Distribution: British Isles, Czechoslovakia, Denmark and Sweden.

XI. LICHENODIPLIS Dyko & D. Hawksw.

in Hawksworth & Dyko, *Lichenologist* **11 :** 51 (1979).

See Hawksworth & Dyko (1979) for further information on this genus.

Type species: Lichenodiplis lecanorae (Vouaux) Dyko & D. Hawksw.

Number of species: Two, both obligately lichenicolous.

Key to the species

1 Conidiomata 50–120 μm diam; conidia 4–7·5 × 2–3 μm . . **Lichenodiplis lecanorae** (p. 38)
– Conidiomata 50–70 μm diam; conidia 9·5–13 × 4–4·5 μm . . **Lichenodiplis lichenicola** (p. 38)

1. Lichenodiplis lecanorae (Vouaux) Dyko & D. Hawksw., *in* Hawksworth & Dyko, *Lichenologist* **11** : 52 (1979).

See Hawksworth & Dyko (1979) for description, illustrations and synonymy.

Hosts: Caloplaca caesiorufa (Wibel) Flagey, *C. cerina* (Ehrh. ex Hedw.) Th. Fr., *C. ferruginea* (Huds.) Th. Fr., *C. flavovirescens* (Wulfen) Dalla Torre & Sarnth., *Evernia prunastri* (L.) Ach., *Lecanora confusa* Almb., *L. dispersa* (Pers.) Sommerf., *L. pallida* (Schreber) Rabenh., *L. polytropa* (Hoffm.) Rabenh., *L. saligna* (Schrader) Zahlbr., *Pertusaria albescens* (Huds.) M. Choisy & Werner and *P.* cf. *leioplaca* DC. Hawksworth & Dyko (1979) also note that there are literature records from *Caloplaca lactea* (Massal.) Zahlbr., *Lecanora expallens* Ach., *L. varia* (Hoffm.) Ach., *Diploschistes scruposus* (Schreber) Norman, *Lecidella elaeochroma* (Ach.) M. Choisy, *Lecidea enteroleuca* Ach., *Micarea nitschkeana* (Lahm ex Rabenh.) Harm. and unidentified *Lecidea* and *Pertusaria* species.

Distribution: Hawksworth & Dyko (1979) saw material from the British Isles, Canary Islands, Denmark, France, Germany, Spain and Sweden; they also noted a literature report from the U.S.S.R. (Novaya Zemyla). Also mentioned from Morocco by Werner (1972 : 95) on *Pertusaria pustulata* f. *glabrata* (Anzi) Hue.

Observations: While examining material in H-NYL in August 1979, I discovered that Nylander had given this species the herbarium name '*Dichaena pertusariae*'; this name does not, however, ever appear to have been used in print.

Specimens (additional to those listed by Hawksworth & Dyko, 1979): **British Isles:** England, S. Devon, Torquay, on *Pertusaria* cf. *leioplaca*, [*?R. Deakin*] [Leighton, *Lich. exs.* no. 245; sub *Opegrapha atra* var. *parella*.] (E!); Westmorland, Brathay church, on *Lecanora* cf. *saligna*, 22 September 1979, *A. Henderson* (herb. Henderson!). Scotland, W. Inverness, Strontian, Horsley Hall, on *Pertusaria albescens* on *Ulmus*, 14 July 1966, *P. W. James* (IMI 237277!). —**France:** Brittany, Brest, on *Pertusaria* cf. *leioplaca*, *Crouan* 135 (H-NYL p.m. 7683!).

2. Lichenodiplis lichenicola Dyko & D. Hawksw., *in* Hawksworth & Dyko, *Lichenologist* **11** : 56 (1979).

See Hawksworth & Dyko (1979) for description, illustrations and a possible synonym.

Host: Rinodina septentrionalis Malme, apothecia.

Distribution: Hawksworth & Dyko (1979) indicated that the type and only known collection of this species came from Finnmark. However, Dr P. M. Jørgensen (*in litt.*) has kindly pointed out that the type almost certainly came from the Yenisey region of the U.S.S.R.

Observations: I have also seen a further collection that may belong to this species (**France:** Vosges, Docelles, on *Pertusaria* cf. *leioplaca*, *J. Harmand*, herb. Vouaux!), with conidia 9–12 × 4–5 μm, but hesitate to refer it definitely to *Lichenodiplis lichenicola* as the conidia are rather thick-walled, much darker brown, and tend to be somewhat broader in relation to their length. Until more collections are available which enable the variability of *L. lichenicola* to be determined, it would be premature to either describe this material as new or state that it definitely belonged here.

XII. LICHENOSTICTA Zopf

Nova Acta Acad. Caesar. Leop. Carol. **70**(4) : 263 (1898).

Conidiomata pycnidial, arising singly, uniloculate, subglobose to broadly pyriform, erumpent to largely superficial, translucent brown to dark brown or black; walls composed of a few layers of intertwined brownish irregular hyphae forming a textura intricata, lined by a hyaline almost pseudoparenchymatous layer of cells, thickened near the ostiole. *Conidiophores* hyaline, irregularly branched, flexuous, multi-septate, arising from the inner

cells of the pycnidial wall. *Conidiogenous cells* enteroblastic, phialidic, sometimes proliferating, integrated into chains, acro-pleurogenous, conidia arising from the apex of a chain and (for other conidiogenous cells) laterally, sometimes polyphialidic, hyaline, cylindrical to doliiform, channel and collarette distinct, narrow proliferating tissue often evident. *Conidia* adhering in slime and extruded as a gelatinous drop, lacriform, distinctly attenuated at the base, hyaline, simple, smooth-walled.

Type species: Lichenosticta alcicornaria (Lindsay) D. Hawksw. (syn. *L. podetiicola* Zopf).

Number of species: Monotypic.

Observations: The generic name *Dendrophoma* Sacc. cannot be used for this species as it is a synonym of *Dinemasporium* Lév., a very different fungus (Sutton, 1968). The catenate arrangement of the conidiogenous cells and details of conidiogenesis show a strong similarity to those of the pycnidia of some lichenized members of the Lecanorales (see Vobis & Hawksworth, 1981). The normal pycnidia of *Cladonia* species have much more regularly branched conidiophores and mainly ellipsoid to bacillariform conidia.

1. Lichenosticta alcicornaria (Lindsay) D. Hawksw., *in* Hawksworth *et al., Lichenologist* **12** : 107 (1980).
(Fig. 19A–G)

Microthelia alcicornaria Lindsay, *Q. Jl microsc. Sci.* II, **9** : 349 (1869).
Type: British Isles, England, Shropshire, Haughmond Hill, on *Cladonia foliacea* (Huds.) Willd., *W. A. Leighton* [*Lich. exs.* no. 15] (E—lectotype!; BM, E—isolectotypes!).
Dendrophoma alcicornaria (Lindsay) Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 283 (1914).
Lichenosticta podetiicola Zopf, *Nova Acta Acad. Caesar. Leop. Carol.* **70**(4) : 263 (1898).
Dendrophoma podetiicola (Zopf) Keissler, *Öst. bot. Z.* **60** : 62 (1910).
Aposphaeria cladoniae Allescher & Schnabl, *in* Allescher, *Ber. Bayer. bot. Ges.* **4** : 32 (1896).
Type: Germany, Munich, Pullach, on *Cladonia fimbriata* (L.) Fr., October 1894, *J. N. Schnabl* (M—holotype!).
Phoma cladoniae (Allescher & Schnabl) Keissler, *Annln naturh. Mus. Wien* **34** : 77 (1921).
?*Aposphaeria cladoniae* var. *floerkeanae* Vouaux, *in* Harmand, *Lich. Fr.* **3** : 335 (1907).

Exsiccatae: Leighton, *Lich. exs.* no. 15 (sub *Cladonia alcicornis;* BM!, E!).—Räsänen, *Lich. fenn. exs.* no. 600 (sub *Dendrophoma alcicornaria**; BM!).

Icones: Lindsay, *Trans. R. Soc. Edinb.* **22:** pl. 8 fig. 3 (1859).—Zopf, *Nova Acta Acad. Caesar. Leop. Carol.* **70**(4) : 264 figs 22–23, 265 figs 24–25 (1898).

Conidiomata pycnidial, immersed or sometimes becoming to $\frac{2}{3}$ erumpent, arising singly, often numerous, scattered, translucent brown to dark brown or black, sometimes shiny, (50–)80–120(–150) μm, subglobose to broadly pyriform, ostiolate; pycnidial wall irregular in outline, mainly 5–10 μm thick but to 20–25 μm thick around the ostiole, composed of 1–3 (or more near the ostiole) irregular layers of intertwined hyphae, hyphae olivaceous brown to dark brown, uneven in diameter, very variable in shape, sometimes strongly inflated between the septa, 3–7 μm wide, thick-walled near the ostiole, inner cells subhyaline and almost pseudoparenchymatous in parts. *Conidiophores* hyaline, irregularly branched, occupying the whole of the pycnidial cavity in young pycnidia, flexuous, multi-septate, arising from the inner cells of the pycnidial wall. *Conidiogenous cells* enteroblastic, phialidic, sometimes percurrently proliferating, integrated into chains, acro-pleurogenous with conidia arising from the apex of a chain and (for other conidiogenous cells) laterally or near a transverse septum, sometimes polyphialidic, hyaline, cylindrical to doliiform, mainly 2·5–4 μm wide and 4–6 μm long, channel and collarette distinct, this (and often

*No. 350, distributed by Räsänen under this name, is not this species but probably an unknown pycnothyriaceous fungus. Mentioned by Sandstede (1931) as present in his *Clad. Exs.* nos. 601, 870–2, and 1574 but these numbers have not been studied by me.

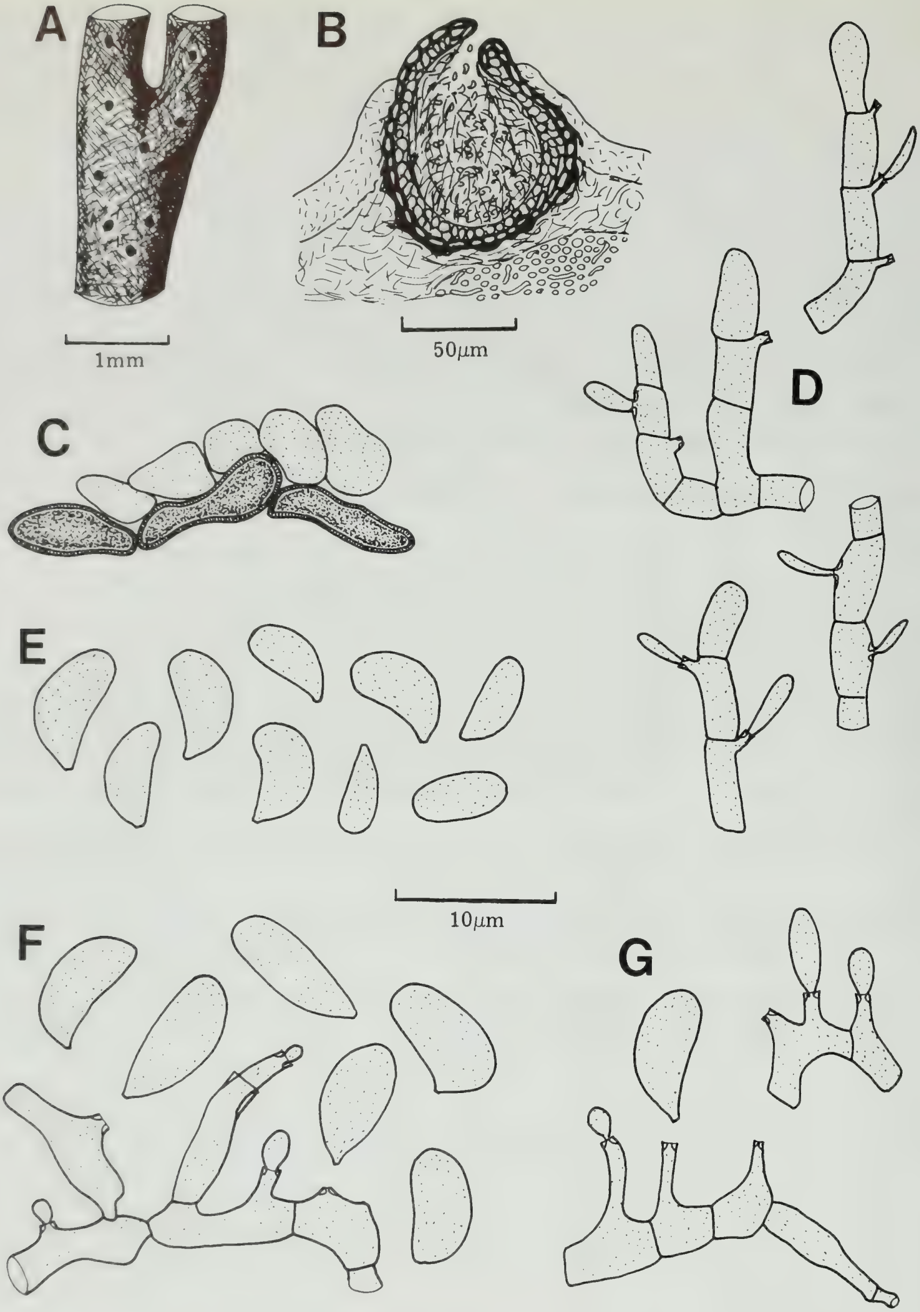

Fig. 19 *Lichenosticta alcicornaria.* **A–E** (Räsänen, *Lich. Exs.* no. 600, K); **A,** pycnidia on podetia of the host; **B,** vertical section of pycnidium; **C,** cells from the pycnidial wall; **D,** chains of conidiogenous cells; **E,** conidia. **F** (*Hafellner 1834*), Conidiogenous cells and conidia. **G** (BM—isotype), Conidiogenous cells and conidia.

conspicuous narrow proliferations) 1–1·5 μm wide. *Conidia* adhering in slime and extruded as a gelatinous drop, lacriform, plano-convex to concavo-convex, rounded at the apex and distinctly attenuated at the base, hyaline, simple, often 1 or more guttulate, smooth-walled, (6–)6·5–10(–11) × (2–)3–4·5(–6) μm.

Hosts: I have examined material on *Cladonia arbuscula* (Wallr.) Rabenh. (*C. sylvatica* auct.), *C. fimbriata* (L.) Fr., *C. foliacea* (Huds.) Willd. and *C. gracilis* (L.) Willd. Also mentioned from *C. cornuta* (L.) Hoffm. by Keissler (1910 : 2), *C. pyxidata* (L.) Hoffm. by Keissler (1930 : 551); from *C. acuminata* (Ach.) Norrlin (*C. norrlinii* Vainio), *C. portentosa* (Dufour) Coem. (*C. impexa* Harm.), and *C. ciliata* var. *tenuis* (Flörke) Ahti by Sandstede (1931 : 52, 76, 340); and from *C. coniocraea* auct. by Folan & Mitchell (1970 : 169). The fungus occurs on both podetia and squamules (especially the lower surfaces) but causes little damage so is easily overlooked. Probably parasymbiotic.

Distribution: Austria (Keissler, 1930 : 551), the British Isles (England; Ireland, Folan & Mitchell, 1970 : 169), Canada (Newfoundland; Keissler, 1910 : 2), Finland, Germany, Italy and Sweden (Keissler, 1910 : 2; Santesson, 1949 : 142).

Observations: The fungus is easily distinguished from other Coelomycetes on *Cladonia* by the characteristic lacriform conidia and catenately arranged acro-pleurogenous conidiogenous cells. Further, it never appears to induce the formation of gall-like growths.

The conidial shape is rather constant in this species but there is a considerable degree of variation in the sizes of conidia between different collections. For example, on a specimen of *C. arbuscula* (IMI 232629!) they measured (8–)9–10(–11) × 4·5–6 μm while on one of *C. gracilis* (*Lich. Fenn. Exs.* no. 600, BM!) they were (6–)6·5–8(–8·5) × 3–4(–5) μm (see Fig. 19E–G). It is thus conceivable that more than a single species might be involved, but in the current state of our knowledge of the variability of *Lichenosticta alcicornaria* it would be imprudent to attempt to recognise two taxa at the present time. The types of both *Aposphaeria cladoniae* and *Microthelia alcicornaria* have conidia in the lower size range, as did that of *Lichenosticta podetiicola* according to the measurements given by Zopf (1898 : 264).

Lindsay (1869*b* : 349) did not provide a description of this species but the name is validly published because he refers to his earlier work (Lindsay 1859 : 161), where a description and illustrations were provided; his epithet must therefore be adopted as it pre-dates that of Zopf. No authentic material of *Lichenosticta podetiicola* could be traced in B (B. Hein, *in litt.*) or M (H. Hertel, *in litt.*), but the figures published by Zopf (1898 : 264–5) leave little doubt the taxa are conspecific, even though Zopf did not show any conidiogenous cells, as the conidia are also of the correct shape and size.

Aposphaeria cladoniae var. *floerkeanae* could not be located amongst Harmand's material in Angers (M. Guerlesquin, *in litt.*) and is not represented in the remnants of Vouaux's herbarium (Rondon, 1970). It was distinguished by conidia 8 × 3 μm so is tentatively retained here as those dimensions are ± within the range of *Lichenosticta alcicornaria* as interpreted here.

Additional specimen: **Italy:** Südtirol, Südtiroler Dolomiten, Passo di Rolle, S Abhänge des Mt Castellazzo, on *Cladonia arbuscula*, 23 October 1976, *J. Hafellner* 1834 (herb. Hafellner!, IMI 232629!).

XIII. **MICROCALICIUM** Vainio [ANAMORPHS]

Acta Soc. Fauna Flora fenn. **57**(1) : 77 (1927).

Conidiomata pycnidial, arising singly or in small groups on the thallus of the host, subglobose, erumpent to almost sessile, with the base to half immersed, dark brown to almost black, ostiolate; walls composed of several layers of pseudoparenchymatous cells, cells in the upper parts of the pycnidium very thick-walled, olivaceous, aeruginose or brown, almost sclerenchymatous, cells in the lower parts of the pycnidium similar or sometimes subhyaline to pale brown, thin-walled, irregular in shape and often almost hyphal in parts. *Conidiophores* absent. *Conidiogenous cells* enteroblastic, lining the pycnidial cavity, acrogenous, subcylindrical to cylindrical, phialidic, with a particularly distinctive often elongate canal, not proliferating, hyaline, smooth-walled. *Conidia* arising singly, not

catenate, subglobose to narrowly ellipsoid, sometimes slightly apiculate at the base, hyaline, simple, thin-walled, smooth-walled, extruded through the ostiole in a mucilaginous drop.

Type species: Microcalicium subpedicellatum (Schaerer) Tibell (syn. *M. disseminatum* (Ach. ex Fr.) Vainio).

Number of species: Four species of *Microcalicium* (Caliciales) were accepted by Tibell (1978) in a critical revision of the genus. Anamorphs are known for two of the species and only these are treated here. Tibell's work should be consulted for information on the teleomorphs.

Observations: No suitable coelomycete generic name could be found for the anamorphs of *Microcalicium* species. I have not introduced a separate generic name for them here because they often (though not exclusively) occur together with the teleomorph, and, when found separately, 'anamorph' can easily be added after the name. Further, as the genus includes lichenized and not only lichenicolous fungi, Art. 59.1 should perhaps be invoked to prevent the introduction of an anamorphic name, as this rule, which permits a dual nomenclature in fungi with pleomorphic life-cycles, specifically excludes (correctly in my view; cf. Hawksworth, 1978*b*: 236–237) lichen-forming taxa.

Key to the species

1 Conidia subglobose, 2–3 × 1·5–2 μm; conidiogenous cells 6–9 × 2–3 μm . . . **Microcalicium subpedicellatum** [anamorph] (p. 42)

– Conidia narrowly ellipsoid, 2–3(–4) × 1·5–2 μm; conidiogenous cells 3–5(–6) × 1·5–2·5 (–3) μm . . . . **Microcalicium conversum** [anamorph] (p. 42)

1. Microcalicium conversum Tibell, *Bot. Notiser* **131 :** 237 (1978) [anamorph].
(Fig. 20G–H)

Icones: Tibell, *Bot. Notiser* **131 :** 242 fig. 7B (1978) [anamorph].

Conidiomata pycnidial, arising singly, subglobose, erumpent to almost sessile or partly immersed, dark brown to black, 40–60(–80) μm wide and 50–80 μm tall; walls 8–12 μm thick, composed of several layers of reddish brown very thick-walled almost sclerenchymatous pseudoparenchymatous cells, becoming somewhat olivaceous in postassium hydroxide, 3–5 μm diam, basal wall apparently similar to the exposed parts at least in almost superficial pycnidia. *Conidiophores* absent. *Conidiogenous cells* enteroblastic, lining the pycnidial cavity, acrogenous, subcylindrical, phialidic, with a distinct and often elongate canal, not proliferating, hyaline, smooth-walled, 3–5(–6) × 1·5–2·5(–3) μm. *Conidia* arising singly, not catenate, narrowly ellipsoid, rounded at the ends, hyaline, simple, thin-walled, smooth-walled, sometimes guttulate, 2–3(–4) × (1–)1·5–2 μm, extruded through the ostiole in a mucilaginous drop.

Hosts: Calicium viride Pers. and *Chaenotheca subroscida* (Eitner) Zahlbr., thalli.

Distribution: The species was recorded by Tibell (*loc. cit.*) only from Argentina (Tierra del Fuego), Australia (Tasmania) and Chile (Magallanes).

Observations: The anamorph of *Microcalicium conversum* is clearly separated from that of *M. subpedicellatum* on the basis of the more complete pycnidial wall, its reddish brown colour, the length of the conidiogenous cells, and the quite different shape of the conidia. The teleomorph also differs from that of *M. subpedicellatum* in having a reddish brown (not greenish) excipulum, and 1 (not 3–7)-septate ascospores (*fide* Tibell, *loc. cit.*).

Specimen: **Chile:** Terr. Magallanes: Rio Rubens, near Hotel Rio Rubens (about 50 km SE of Natales), on *Calicium viride* on *Nothofagus pumila*, 13 January 1941, *R. Santesson* 5618 p.p. (S!).

2. Microcalicium subpedicellatum (Schaerer) Tibell, *Bot. Notiser* **131 :** 240 (1978) [anamorph].
(Fig. 20A–F)

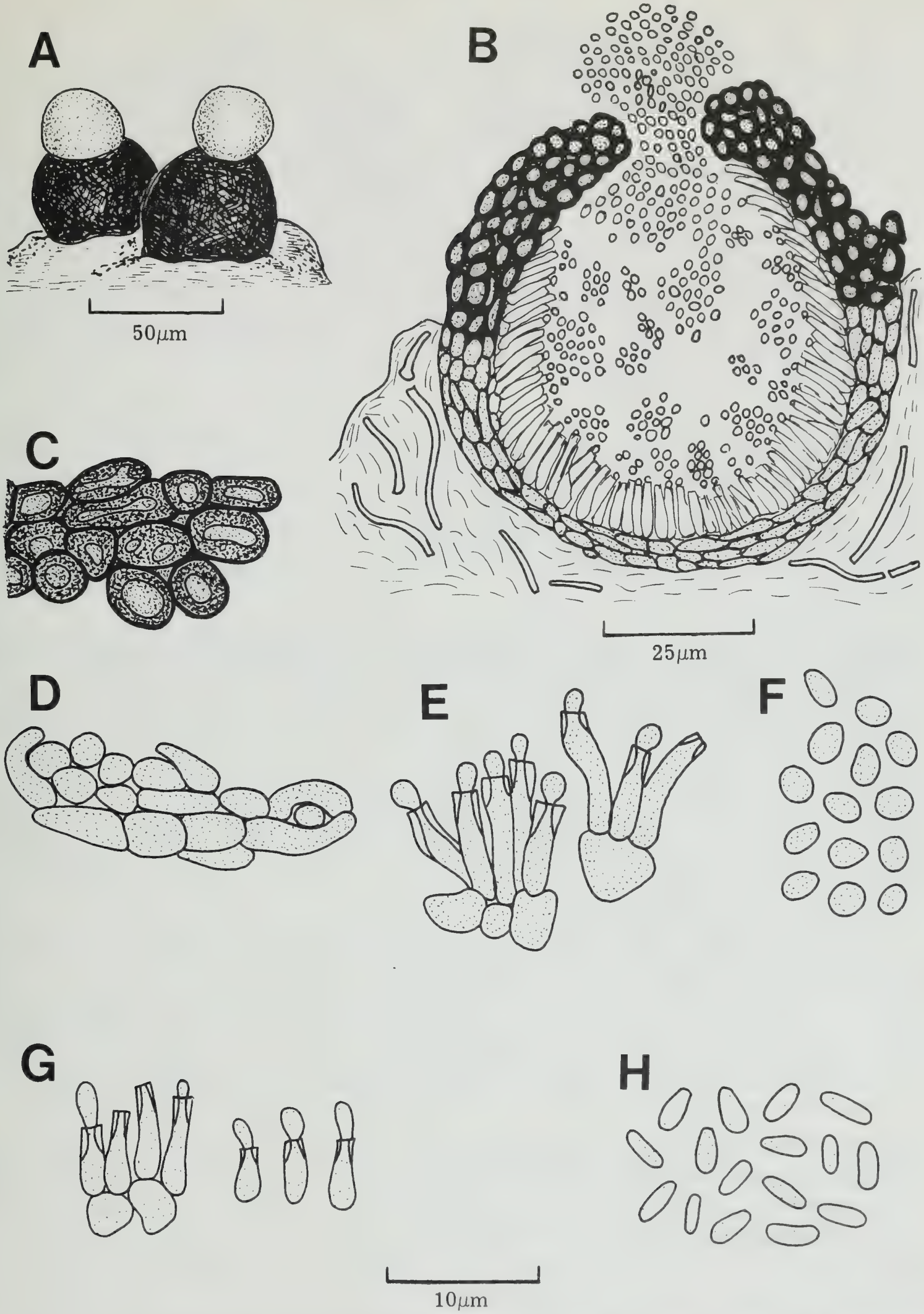

Fig. 20A–F, *Microcalicium subpedicellatum* [anamorph] (*Hafellner 1095*); **A,** pycnidia on the host thallus; **B,** vertical section of pycnidium; **C,** cells from the upper part of the pycnidial wall; **D,** cells from the lower part of the pycnidial wall; **E,** conidiogenous cells; **F,** conidia. **G–H,** *M. conversum* [anamorph] (*Santesson 5618* p.p); **G,** conidiogenous cells; **H,** conidia.

Icones: Tibell, *Bot. Notiser* **131** : 245 fig. 10B, 246 fig. 11 (1978) [anamorph].

Conidiomata pycnidial, subglobose, arising singly or in small groups, erumpent with the lower $\frac{1}{3}$-$\frac{1}{2}$ remaining immersed, black, 40–60 μm diam; walls in the upper parts mainly 10–15 μm thick, composed of several layers of somewhat aeruginose very thick-walled almost sclerenchymatous pseudoparenchymatous cells, becoming brownish in potassium hydroxide, 3–5 μm diam, walls in the lower parts 5–8 μm thick, composed of 2–3 layers of thinner-walled subhyaline cells forming an irregularly pseudoparenchymatous to in places almost hyphal tissue. *Conidiophores* absent. *Conidiogenous cells* enteroblastic, lining the pycnidial cavity, acrogenous, subcylindrical to cylindrical, phialidic, with a distinctly thickened and elongate canal, not proliferating, hyaline, smooth-walled, 6–9 × 2–3 μm. *Conidia* arising singly, not catenate, subglobose, sometimes slightly pointed at the base, hyaline, simple, thin-walled, smooth-walled, 2–3 × 1·5–2 μm, extruded through the ostiole in a milky-white mucilaginous drop.

Hosts: Calicium glaucellum Ach., *C. viride* Pers., *Chaenotheca brunneola* (Ach.) Müll. Arg., *C. chrysocephala* (Turner ex Ach.) Th. Fr., *C. subroscida* (Eitner) Zahlbr., *C. trichialis* (Ach.) Th. Fr., and undetermined Caliciales, thalli. A parasitic species in which the pycnidia colonize at an early stage with to 15 per host areole. Infected thalli are eventually decolourized and may turn brownish with the formation of extensive lesions in the colonies. Sometimes apparently growing directly on lignum or with other algae, perhaps persisting *in situ* after the loss of the host in such cases.

Distribution: Circumboreal. Recorded by Tibell (*loc. cit.*) from Austria, the British Isles (Scotland), Canada, France, Italy, Norway, Sweden, Switzerland and the USSR.

Observations: The separation of this species from the anamorph of *M. conversum* is discussed under that species above.

Specimens: **Austria:** Steiermark, Ostalpen, Gurktaler Alpen, Frauenalm S von Murau, on *Chaenotheca trichialis*, 18 June 1978, *J. Hafellner* 3899 (GZU!). —**Italy:** Südtirol, Mendelgebirge, Penegal SW von Bozen, on *C. chrysocephala*, 20 October 1975, *J. Hafellner* 1095 (GZU!); *loc. cit.*, on *Chaenotheca* sp., 20 October 1975, *J. Poelt & J. Hafellner* 1094 (GZU!); *loc. cit.*, on *Chaenotheca* sp., 20 October 1975, *J. Hafellner* 1084 (GZU!).

XIV. **MINUTOPHOMA** D. Hawksw. **gen. nov.**

Genus lichenicola ad Coelomycetes Sphaeropsidales pertinens. Conidiomata singularia, uniloculata, dispersa, globosa vel subglobosa, semi-immersa, nigra, cum muris textura angulari sed inferiore solum ex cellulis conidiogenis, ostiolata. Conidiophora desunt. Cellulae conidiogenae enteroblasticae, acrogenae, ampulliformes vel breve ampulliformes, phialidicae, non prolifericae, hyalinae sed basi plerumque pallide brunneae. Conidia subcylindrica, hyalina, simplicia, laevia, minutissima.

Conidiomata pycnidial, arising singly, scattered, globose to subglobose, half-immersed, black; walls composed of thick-walled dark brown cells forming a textura angularis above, these cells readily separating, the lower part consisting only of the conidiogenous cells, the upper cells separating to form an irregular ostiole. *Conidiophores* absent. *Conidiogenous cells* enteroblastic, forming the lower part of the pycnidial wall, acrogenous, ampulliform to shortly ampulliform, phialidic, not proliferating, hyaline but with the base often pale brown. *Conidia* not adhering, not catenate, subcylindrical, rounded at the apices, hyaline, simple, smooth-walled, minute.

Type species: Minutophoma chrysophthalmae D. Hawksw. (holotypus).

Number of species: Monotypic.

Observations: Minutophoma is most closely allied to *Phoma* (see p. 49), but differs in the extremely small size of the pycnidia and some other important respects: the thick-walled angular cells tending to separate around an irregular ostiole, the absence of a differentiated wall in the immersed part of the pycnidium, the conidiogenous cells tending to be more

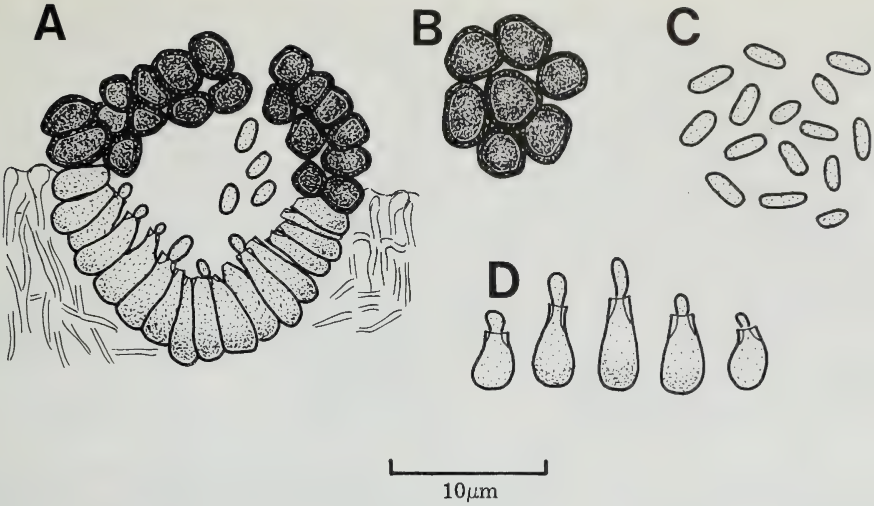

Fig. 21 *Minutophoma chrysophthalmae* (IMI 237276—holotype). **A,** Vertical section of pycnidium. **B,** Surface view of cells from the upper part of the pycnidium which easily separate. **C,** Conidia. **D,** Conidiogenous cells.

elongated and also pigmented below, and the extremely small conidia. An additional feature might be the absence of a very deeply pigmented area around the ostiole, but this is not emphasized here because the whole of the exposed part of the pycnidium in *M. chrysophthalmae* might be considered as equivalent to this zone.

The separation of *Asterophoma* from *Minutophoma* is discussed above (p. 8).

1. Minutophoma chrysophthalmae D. Hawksw. **sp. nov.**
(Fig. 21A–D)

Fungus lichenicola. Conidiomata singularia, uniloculata, dispersa, globosa vel subglobosa, semi-immersa, nigra, 20–40 μm diam, cum muris textura angulari 5–8 μm latis e cellulis atrobrunneis 3–4 μm diam sed inferiore solum ex cellulis conidiogenis; ostiolata. Conidiophora desunt. Cellulae conidiogenae enteroblasticae, acrogenae, ampulliformes vel breve ampulliformes, phialidicae, non prolifericae, hyalinae sed basi plerumque pallide brunneae, 3·5–6 × 2–3·5 μm. Conidia subcylindrica, hyalina, simplicia, laevia, 2–3·5 × 1·5 μm.

Typus: Magna Britannica, Scotia, E. Inverness, Glen Affric, Coille Ruigh na Cuileige, in apotheciis *Chrysothrix chrysophthalmae* (P. James) P. James & Laundon e ligno *Pini,* 18. vi. 1976, *B. J. Coppins* 3196 p.p. (IMI 237276—holotypus!; E—isotypus!).

Conidiomata pycnidial, semi-immersed, sometimes becoming erumpent and almost superficial, scattered over the surface of the host apothecia, arising singly, black, 20–40 μm diam; wall in the exposed part of the pycnidium composed of 2–3 layers of cells, 5–8 μm thick, dark brown, cells thick-walled, pseudoparenchymatous, tending to be angular, not radially compressed, readily separating in squash preparations, 3–4 μm diam, the upper cells separating to form an irregular ostiole, the lower part of the pycnidium composed almost exclusively of conidiogenous cells, the basal parts of which become slightly pigmented. *Conidiogenous cells* enteroblastic, forming the lower part of the pycnidial wall, arranged in a single layer, acrogenous, ampulliform to shortly ampulliform, phialidic, not proliferating, mainly hyaline to subhyaline but with the base often pale brown, 3·5–6 × 2–3·5 μm. *Conidia* abundantly produced, subcylindrical, rounded at the apices, not adhering, not catenate, hyaline, simple, not distinctly guttulate, smooth-walled, 2–3·5 × 1–1·5 μm.

Host: Chrysothrix chrysophthalma (P. James) P. James & Laundon (syn. *Micarea chrysophthalma* P. James), apothecia. Infected apothecia are often richly covered by

pycnidia but otherwise retain their characteristic bright yellow-green appearance and continue to produce ascospores. The species consequently has to be interpreted as a parasymbiont rather than a parasite.

Distribution: British Isles (Scotland).

Observations: A distinctive species which, despite the minute size of the pycnidia, is easily detected by their black colour contrasting markedly with that of the host's apothecia. As a result of its small size and the minute conidia, *Minutophoma chrysophthalmae* is unlikely to be confused with the other taxa treated in the present revision.

Additional specimens: **British Isles:** E. Inverness, Guisachan Forest, south-west of Garve Bridge, on *Chrysothrix chrysophthalma* on *Pinus* lignum, 26 May 1975, *B. J. Coppins et al.* 1955 (E!); E. Ross, Amat Forest, on *Chrysothrix chrysophthalma* on *Pinus* lignum, 28 May 1975, *B. J. Coppins (& F. Rose)* 2225 (E!).

XV. NIGROPUNCTA D. Hawksw. gen. nov.

Genus lichenicola ad Coelomycetes Sphaeropsidales pertinens. Conidiomata singularia, uniloculata, dispersa, subglobosa ad cupuliformia, immersa, plusminusve hyalina, cum muris textura intricata, late ostiolata. Conidiophora non vel sparse ramosa, hyalina, septata, e cellulis plusminusve isodiametricis. Cellulae conidiogenae holothallicae, acrogenae, integratae, terminales, determinatae, subglobosae ad subcylindrices, hyalinae vel ad apicem olivaceae. Conidia catenata, in cirrhum accumulata, irregulariter, e cellulis numerosis composita, cellulis subglobosis vel angularibus, atro-olivacea vel nigra, plerumque simplicibus, rugulosa.

Conidiomata pycnidial, arising singly, subglobose at first but becoming cupuliform with age, immersed, ± hyaline, largely obscured by the mass of conidia; walls composed of loosely interwoven hyaline hyphae forming a textura intricata. *Conidiophores* forming a compact layer lining the inner wall of the pycnidial cavity, not or sparsely branched, hyaline, septate, composed of ± isodiametric cells. *Conidiogenous cells* holothallic, acrogenous, integrated, terminal, determinate, subglobose to subcylindrical, hyaline but becoming olivaceous at the apex. *Conidia* catenate at first, accumulating in a cirrhus, irregular, composed of numerous subglobose to angular cells, dark olivaceous or black, individual cells mainly simple, rough-walled.

Type species: Nigropuncta rugulosa D. Hawksw. (holotypus).

Number of species: Monotypic.

Observations: This genus appears to have no close allies amongst the non-lichenicolous fungi. The method of conidiogenesis and the aggregation of cells to form multicellular propagules recalls that seen in the lichenicolous hyphomycete genus *Sclerococcum* Fr. ex Fr. (Hawksworth, 1975*a*, 1979), but there the conidiogenous cells are arranged in superficial sporodochia and the conidia are smooth-walled. Amongst the lichenicolous Coelomycetes, there is some slight similarity to *Vouauxiella uniseptata* (see p. 66) but in that taxon the conidiogenous cells are much longer and pigmented, the conidia are consistently 1-septate, not aggregating into multi-cellular clumps, have a different type of ornamentation, and are produced in a pycnidium with a pigmented and cellular wall.

The generic name proposed recalls the black-spotted appearance imparted to the host thallus.

1. Nigropuncta rugulosa D. Hawksw. sp. nov.
(Figs. 22A–D, 23A–C)

Fungus lichenicola. Conidiomata singularia, uniloculata, dispersa, subglobosa ad cupuliformia, immersa, plusminusve hyalina, 100–450 μm lata, cum muris textura intricata 10–20 μm latis, e hyphis hyalinis 2·5–3 μm latis, late ostiolata. Conidiophora non vel sparse ramosa, hyalina, septata, 10–15 × 2–3·5 μm, e cellulis isodiametricis. Cellulae conidiogenae holothallicae, acrogenae, integratae, terminales, determinatae, subglobosae vel subcylindrices, hyalinae vel ad apicem interdum olivaceae,

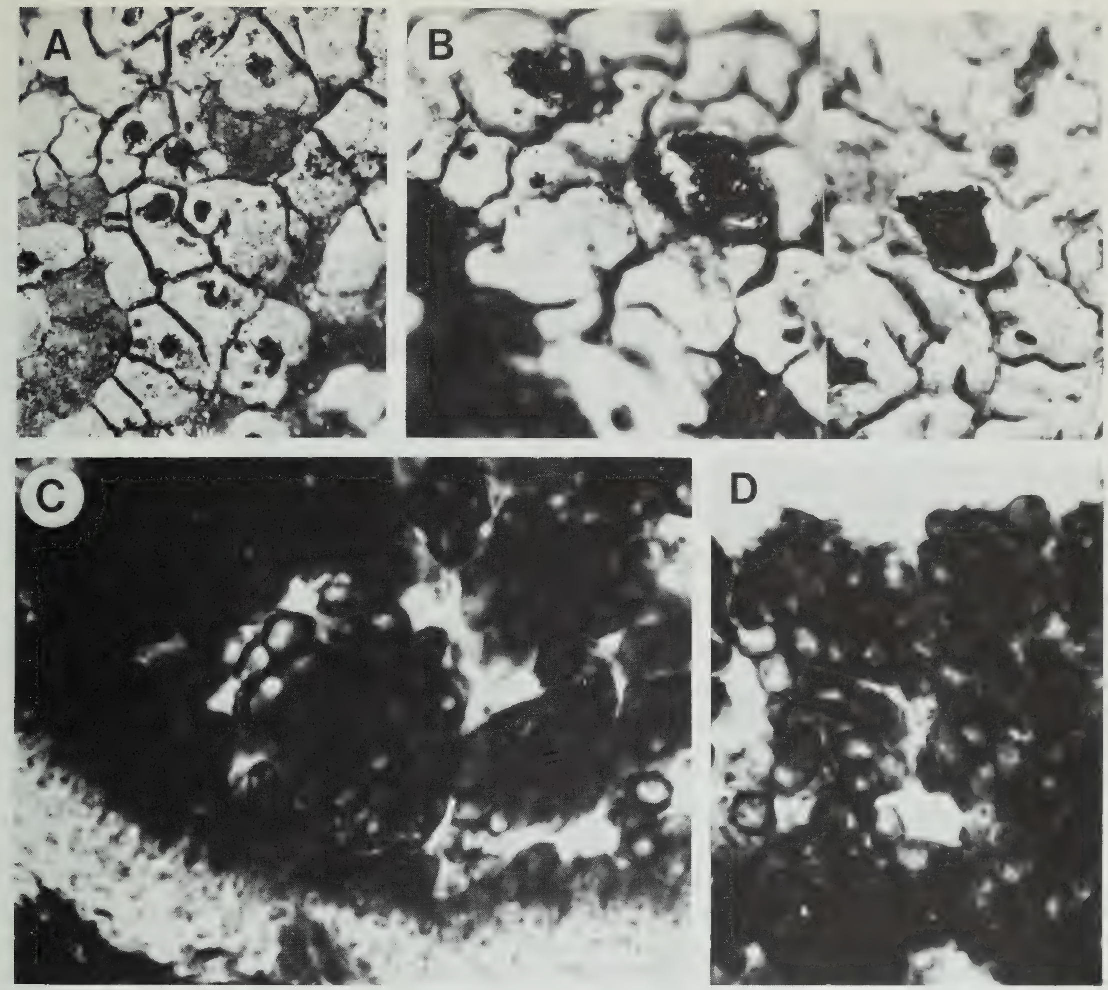

Fig. 22 *Nigropuncta rugulosa* (IMI 241409—holotype). **A,** Infected areolae (× 30). **B,** Infected areolae showing the emergent conidial masses (× 80). **C,** Vertical section of pycnidium (lower part) to show the pycnidial wall and conidiogenous cells (× 1020). **D,** Conidia (× 1020).

3–4 μm latae, Conidia catenata, in cirrhum accumulata, irregulariter, e cellulis numerosis composita, plerumque 20–40 μm diam, atro-olivacea vel nigra, cellulis subglobosis vel angularibus, plerumque simplicibus, rugulosis, plerumque 6–8 μm diam.

Typus: Austria, Steiermark, Schladminger Tauren, Kleinsölk-Obertal, west. Abhänge der Kesselspitze, alt. 1700 m, in thallo lichenis ignoti e saxis schistosis, 12. viii. 1974, *J. Hafellner* 3929 (IMI 241409—holotypus!; herb. Hafellner—isotypus!).

Conidiomata pycnidial, arising singly, immersed in areolae of the host, the adjacent thalline tissue sometimes proliferating to form a distinct raised margin around the spore mass which recalls a thalline exciple, only exceptionally more that one pycnidium in each areole, ± hyaline but black when viewed from above as a result of the dense spore mass, 100–450 μm wide; ostiolate, the ostiole ± equal to the width of the pycnidium in older conidiomata, mainly ± circular but the margin sometimes invaginated or angular, not clearly differentiated but forming by an irregular opening caused by an expansion of the pycnidium, the pycnidia are at first subglobose or flask-shaped but become cupulate to almost acervular with age; walls poorly demarcated from the host tissues, mainly hyaline but sometimes becoming olive-tinged, especially towards the upper parts, 10–20 μm thick, the

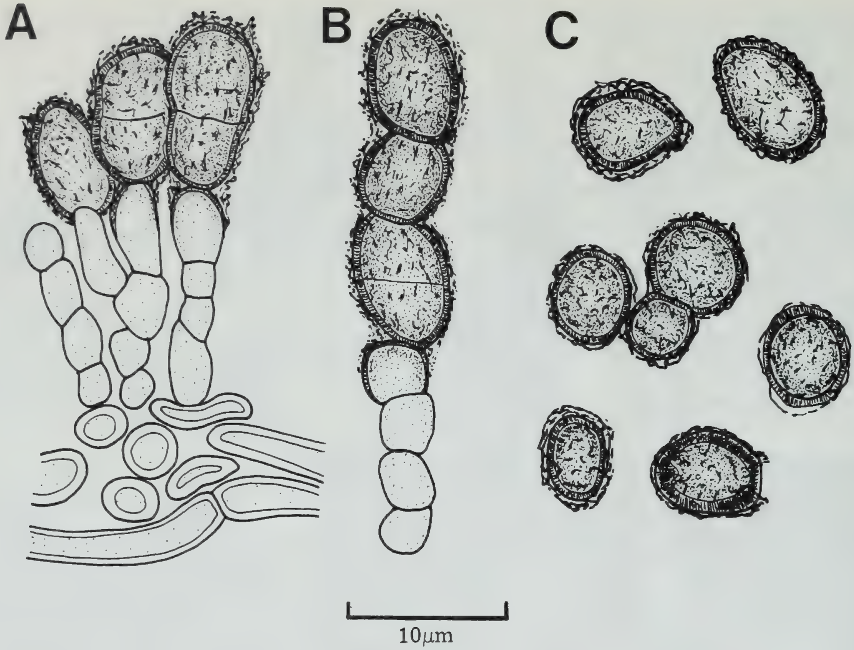

Fig. 23 *Nigropuncta rugulosa* (IMI 241409—holotype). **A,** Conidiogenous cells and detail of pycnidial wall. **B,** Conidiogenous chain with developing conidia. **C,** Cells squashed from the irregular multicellular conidia.

outer part composed of 2–5 irregular layers of loosely to moderately compacted interwoven hyphae, hyphae thick-walled, hyaline, 2·5–3 μm wide, inner part comprising thinner-walled mainly isodiametric loosely packed pseudoparenchymatous cells, 2–3·5 μm diam, these scarcely distinguishable from conidiophores. *Conidiophores* forming a compact layer lining the inner wall of the pycnidial cavity, simple or sparsely branched, arranged ± parallel to one another, hyaline, septate, 10–15 × 2–3·5 μm, composed of almost isodiametric cells, somewhat constricted at the septa. *Conidiogenous cells* holothallic, integrated, terminal, determinate, subglobose to subcylindrical, resembling the conidiophore cells but sometimes becoming olivaceous at the apex, 3–4 μm wide. *Conidia* arising in short basipetal chains, tightly adhering to those produced from adjacent conidiogenous cells to form multicellular propagules, these very irregular in shape but mainly 20–40 μm overall, deep olive to almost black, extruded through the ostiolar opening as a dense black cirrhus which is clearly seen with a × 10 lens, individual cells mainly simple, thick-walled, subglobose to angular through compression by adjacent cells, walls roughened with a very irregular granular-lacerate ornamentation, this perhaps originating from exfoliating layers of wall tissue, cells mainly 6–8 μm diam.

Host: On an unidentified sterile grey areolate crustose lichen thallus. The areolae are not discoloured in any way and algal cells close to the pycnidia retain their usual colour also. The species is evidently parasymbiotic rather than parasitic, but could even be lichenized (see below).

Distribution: Austria. Known only from the type collection with certainty, but perhaps also present in Germany (see below).

Observations: This is a most distinctive species macroscopically and superficially recalling *Thelomma siliceum* (Fée) Tibell (see Tibell, 1976: figs. 15–16); however, microscopic examination soon reveals that it is not an ascomycete.

Within the host thallus, it seem impossible to distinguish hyphae of the pycnidium from

those forming the tissues of the host. Further, most areolae have only a single pycnidium and the pycnidia are evenly distributed over the material, and not in any way localized. These facts, together with the consideration that the thallus and its algae are maintained in a healthy condition, makes it necessary to speculate whether the present fungus is actually an independent lichenized coelomycete. In the absence of additional material for study and detailed ultrastructural investigations, it seems impossible to resolve this question at the present time.

One factor which may support the parasymbiotic thesis is a report of what may be the same fungus on *Lecanora alphoplaca* (Wahlenb.) Ach. by Gerber (1931 : 481 figs. 14–15). This author illustrated an unnamed fungus on this host collected by Zopf at 'Oberwinkel in Gröden' which has some important similarities to *Nigropuncta rugulosa,* particularly in the macroscopic appearance of the infection and the formation of dark-coloured multicellular conidia which were very irregular in shape and composed of subglobose to angular cells. Interestingly, he appears to have considered the structure referred to above called the pycnidial wall as the invaginated cortical layer of the host. I have not been able to locate the material Gerber studied, and from his paper alone cannot confidently assert that he had the same taxon because sufficient information on dimensions and conidium formation was not provided. If the two are conspecific, however, as Gerber had a host he could determine, then *N. rugulosa* must be considered a parasymbiont and not an independent lichen.

The dark olive colour of the conidia is particularly characteristic and must be due to a pigment (or pigments) different from those present in other dark-spored lichenicolous Coelomycetes. The lacerate-granulose roughening of the conidia is also an unusual feature. This may conceivably originate either from an exfoliation of the conidial wall layers, or be wall remnants produced during conidiogenesis. The pigmentation precludes a more detailed light microscopic study, and ultrastructural investigations are needed to firmly determine the nature of this roughening and any relationship it might have to the process of conidiogenesis.

XVI. **PHOMA** Sacc. nom. cons.

Michelia **2:** 4 (1880).

See Sutton (1980 : 378) for generic synonyms.

Conidiomata pycnidial, arising singly or aggregated, globose, immersed or partly erumpent, brown to dark brown, ostiolate; walls usually thin, composed of a few layers (often 1–3) of cells, cells pseudoparenchymatous, pale brown to brown, more deeply pigmented around the ostiole in many species, rather thin-walled, textura angularis. *Conidiophores* normally absent. *Conidiogenous cells* enteroblastic, lining the pycnidial cavity, short-cylindrical to doliiform, phialidic, not proliferating, hyaline. *Conidia* arising singly, not catenate, variable in shape in different species, ellipsoid, subcylindrical, fusiform, pyriform or globose, rounded at the apex and base or with the base slightly truncated, hyaline, simple when mature (exceptionally becoming 1-septate), sometimes distinctly guttulate, thin-walled, smooth-walled.

Type species: Phoma herbarum Westend.

Teleomorph (perfect states): A wide range of loculoascomycetes are described as having anamorphs referrable to *Phoma,* including species of *Leptosphaeria* Ces. & de Not. and *Pleospora* Rabenh. ex Ces. & de Not. Most *Phoma* species, however, remain unconnected to teleomorphs.

Number of species: According to Sutton (*loc. cit.*) many more than 2000 species have been described in this genus, which was traditionally employed for all caulinicolous Coelomycetes with small, hyaline, simple conidia. The genus is now employed for species from many habitats (and includes taxa from a very wide range of substrates) and perhaps really should only include about 50 species; a key to 27 is included in Sutton (*loc. cit.*). Five lichenicolous species are now known.

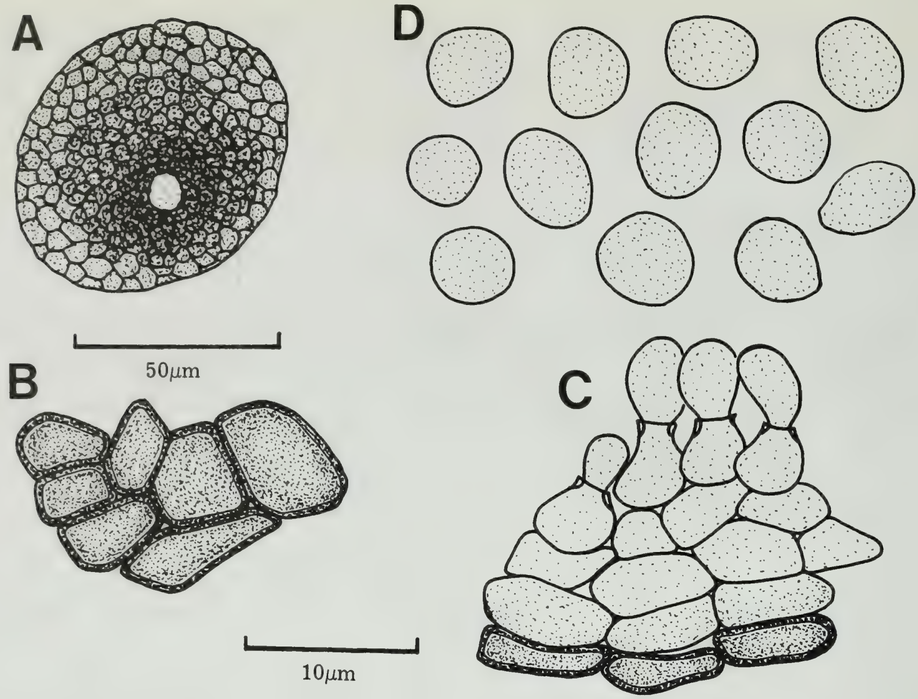

Fig. 24 *Phoma caloplacae* (UPS—holotype). **A,** Surface view of pycnidium. **B,** Surface view of pycnidial wall. **C,** Conidiogenous cells and pycnidial wall. **D,** Conidia.

Observations: Phoma-like fungi on lichens have often been placed in *Phyllosticta* Pers. ex Desm., a genus formerly adopted for similar fungi on leaves as opposed to stems, presumably in the belief that lichen thalli approximated more closely to 'leaves' than 'stems'. The type species of *Phyllosticta,* however, is in any case very different, conforming to the concept of *Phyllostictina* Sydow, and can not be used for such fungi (Punithalingam, 1974 : 60–61). The lichenicolous species referred to *Phoma* here agree closely with the concept of *Phoma* adopted by Sutton (*loc. cit.*).

Modern work on species concepts in *Phoma* has emphasized studies of their behaviour in pure culture and it would obviously be of interest to obtain the lichenicolous species in culture and then compare the isolates with the known non-lichenicolous taxa.

Key to the lichenicolous species

1 Conidia broadly to narrowly ellipsoid 2
– Conidia subglobose, (4–)5–6(–7) μm diam; on *Caloplaca cerina* . . **Phoma caloplacae** (p. 50)

2(1) Conidia narrowly ellipsoid, usually less than 2·5 μm wide 3
– Conidia broadly ellipsoid, 4–5·5(–6) × 2·5–3·5(–4) μm; on *Physcia aipolia* and *Physconia pulverulacea* . . . . **Phoma physciicola** (p. 56)

3(2) Conidia to 2 μm wide 4
– Conidia (4–)4·5–6(–7) × 2–2·5(–3) μm; on *Peltigera malacea* . . . **Phoma peltigerae** (p. 54)

4(3) Conidia 5–7 × 1·5–2 μm; on *Parmelia* species . . . . . . **Phoma cytospora** (p. 51)
– Conidia 3·5–5 × 1·5–2 μm; on an *Usnea* species . . . . **Phoma dubia** (p. 53)

1. Phoma caloplacae D. Hawksw. **sp. nov.**
(Fig. 24A–D)

Fungus lichenicola. Conidiomata singularia, uniloculata, dispersa, subglobosa, immersa sed erumpescentia, atrobrunnea, (50–)70–100(–130) μm lata, cum muris textura angulari usque 10–15 μm

latis, e cellulis 5–8 × 3–4 μm. Cellulae conidiogenae enteroblasticae, acrogenae, subglobosae vel late obpyriformes, phialidicae, non prolifericae, hyalinae, 5–6 μm diam. Conidia subglobosa, hyalina, simplicia, laevia, (4–)5–6(–7) μm diam.

Typus: U.S.S.R., Guv. Jenisejsk, Stolba, lat. bor. 60°20′N, in apotheciis *Caloplacae cerinae* (Ehrh. ex Hedw.) Th. Fr., 1. vii. 1876, *M. Brenner* 1027b p.p. (UPS—holotypus!).

Conidiomata pycnidial, immersed at first, the upper $\frac{1}{3}$ erumpent at maturity, arising singly, scattered, dark brown, subglobose, (50–)70–100(–130) μm diam, ostiolate, cells surrounding the ostiole dark brown, darker than the remaining wall which is subhyaline to pale brown; wall 3–5 layers of cells thick, 10–15 μm thick, cells pseudoparenchymatous, the outermost brown to dark brown with the walls thickened, the inner subhyaline with thinner walls, generally somewhat radially compressed and angular, 5–8 μm diam in surface view and mainly 3–4 μm thick in section. *Conidiogenous cells* arising from the inner wall of the pycnidium, lining the pycnidial cavity, subglobose to broadly obpyriform, hyaline, smooth-walled, phialidic, not proliferating, 5–6 μm diam. *Conidia* abundant, subglobose but often somewhat angular due to mutual compression within the pycnidial cavity, hyaline, simple, sometimes guttulate, smooth-walled, (4–)5–6(–7) μm diam.

Host: Caloplaca cerina, apothecia. Infected discs become discoloured dark brown to blackish and ascospore production is inhibited by the presence of the fungus.

Distribution: U.S.S.R. Known only from the type collection.

Observations: Readily separated from the other species accepted in the genus by the subglobose to angular, and not ellipsoid, conidia.

2. Phoma cytospora (Vouaux) D. Hawksw., *Trans. Br. mycol. Soc.* **67** : 56 (1976). (Fig. 25A–C)

Phyllosticta cytospora Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 193 (1914).
Type: France, Blainville, on *Parmelia caperata,* 4 March 1906, *M. Missie* (herb. Vouaux—neotype!).

Icones: Hawksworth & Punithalingam, *Trans. Br. mycol. Soc.* **61** : 62 fig. 4 (1973).

Conidiomata pycnidial, immersed, arising singly or more commonly in groups, scattered, black, subglobose, 40–80 μm diam, ostiolate; wall 2–3 layers of cells thick, mainly 7–10 μm thick but to about 15 μm near the ostiole, brown to dark brown, cells pseudoparenchymatous, not markedly radially compressed, 5–7 μm long and 3–4 μm tall, the inner cells subhyaline to pale brown and with somewhat thinner walls. *Conidiogenous cells* arising from the inner wall of the pycnidium, lining the pycnidial cavity, subglobose to broadly obpyriform, hyaline, smooth-walled, phialidic, not proliferating, 2–3 × 1–2 μm. *Conidia* abundant, narrowly ellipsoid to slightly curved, one apex slightly truncated, hyaline, simple, sometimes 1–2 guttulate, smooth-walled, 5–7 × 1·5–2 μm.

Hosts: Parmelia caperata (L.) Ach., *P. laevigata* (Sm.) Ach., *P. perlata* (Huds.) Ach., *P. reticulata* Taylor, and *P. sulcata* Taylor, thalli. Necrotic decolourized patches 1–4 mm diam are formed, each of which includes 5–18 pycnidia, the boundary with healthy tissue being marked by a blackened zone of tissue 100–250 μm wide; the patches are usually discrete and damage localized but occasionally they may coalesce, particularly on *P. reticulata,* killing large areas of the thallus. Reported by Vouaux (1914) and Keissler (1930) only on *P. caperata.*

Distribution: British Isles, France, and possibly Germany (see p. 83).

Observations: The decolourized necrotic patches produced by this species recall those formed on the same or allied hosts by *Cornutispora lichenicola* and *Lichenoconium erodens.*

Phyllosticta cytospora was originally described from material of *Parmelia caperata* collected in the 'Forêt de Vitrimont en Meurthe-et-Moselle' by Vouaux. This material is no longer present in Vouaux's herbarium (Rondon, 1970) but there is a further collection made

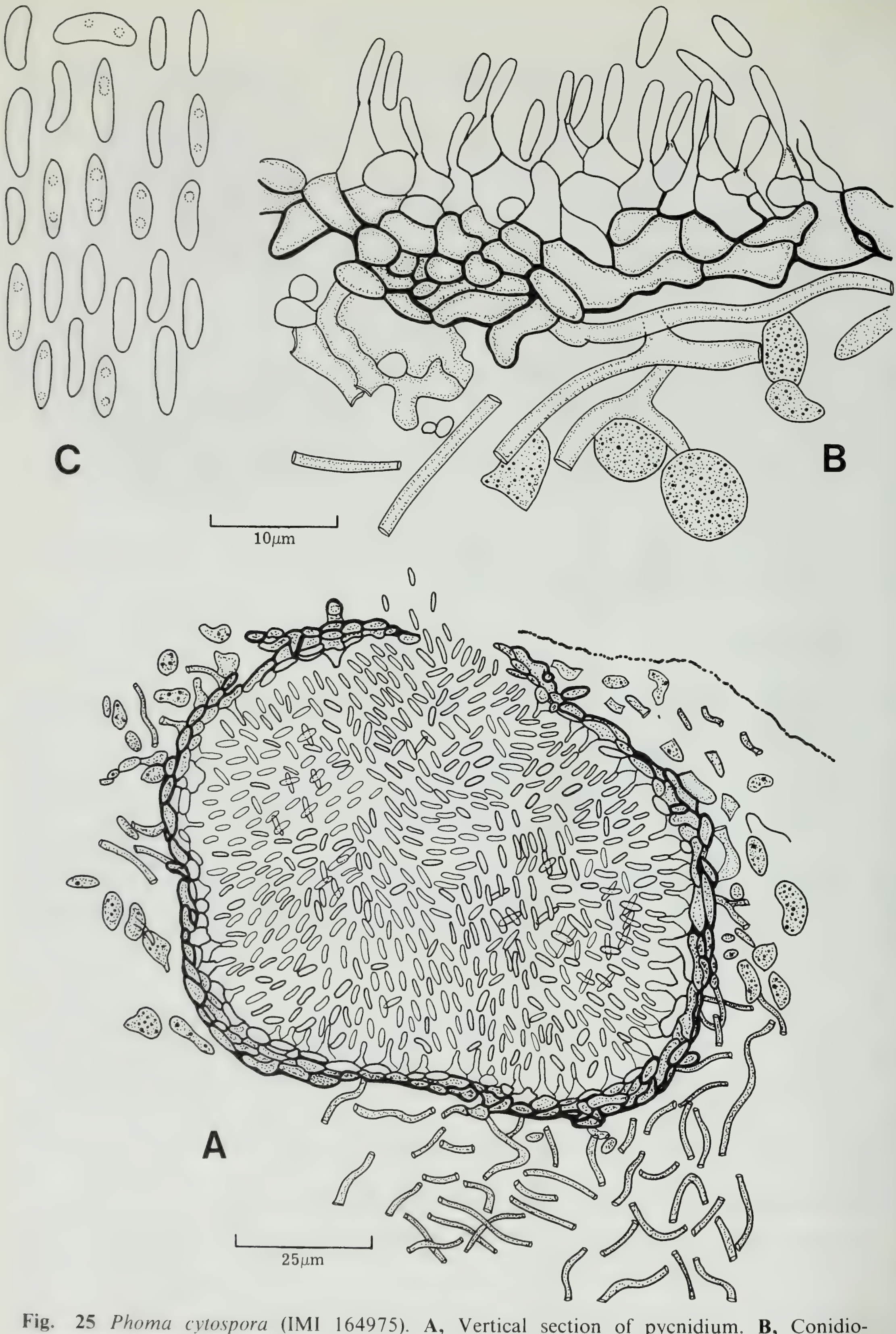

Fig. 25 *Phoma cytospora* (IMI 164975). **A**, Vertical section of pycnidium. **B**, Conidiogenous cells and pycnidial wall. **C**, Conidia. Reproduced from Hawksworth & Punithalingam (1973 : 62).

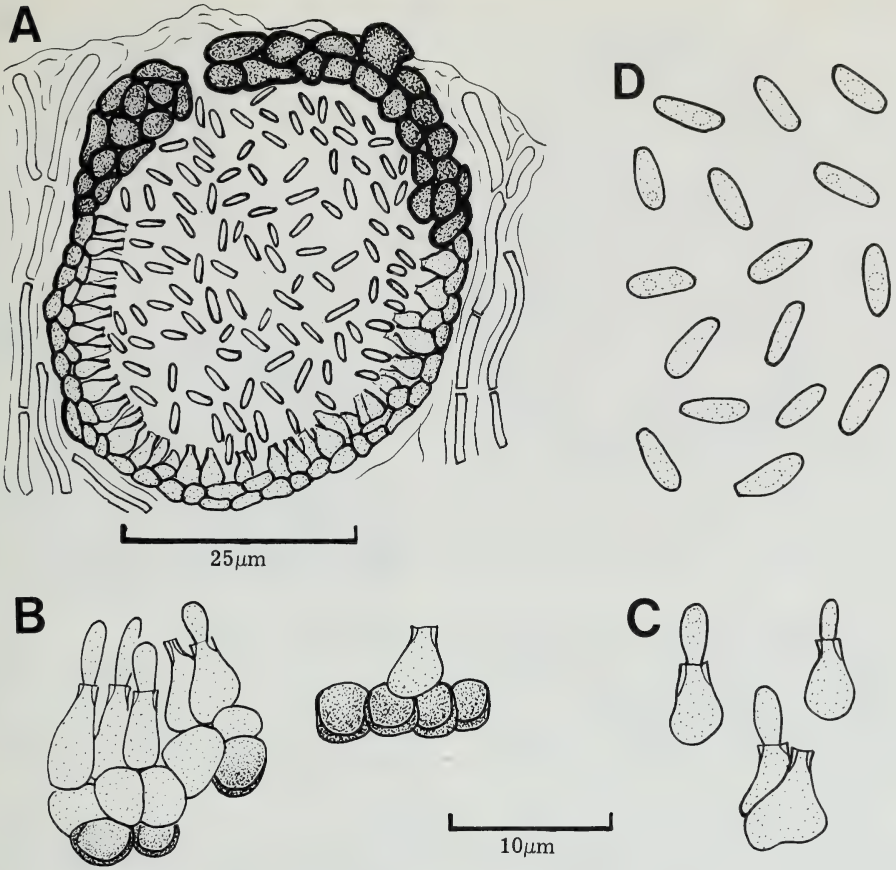

Fig. 26 *Phoma dubia* (E—holotype). **A,** Vertical section of pycnidium. **B,** Conidiogenous cells and pycnidial wall. **C,** Conidiogenous cells. **D,** Conidia.

at Blainville in 1906 labelled *'Phyllosticta cytospora* mihi' present which agrees in all details with Vouaux's original description and later collections; the Blainville specimen is consequently designated as neotype for this name here.

The name *Phyllosticta lichenicola* Allescher may have been partly based on a fungus very close to *Phoma cytospora* (see p. 83). *Phoma caperatae* Vouaux, however, seems unlikely to represent *P. cytospora* (see p. 80).

Additional specimens: **British Isles:** England, S. Devon, Slapton Ley Nature Reserve, on *Parmelia perlata* on *Quercus,* 30 March1972, *D. L. Hawksworth* 2695 (IMI 164975!), *loc. cit.,* on *P. reticulata* on *Acer pseudoplatanus,* 25 August 1978, *D. L. Hawksworth* 4772 (IMI 231655!), *loc. cit.,* on *P. sulcata,* 25 August 1976, *D. L. Hawksworth* 4322 (IMI 206364!); S. Devon, Killerton Park, on *P. reticulata* on *Quercus,* 3 September 1978, *D. L. Hawksworth* 4849 (IMI 231732!); S. Devon, Start Point, nr Langerstone Point, on *P. perlata* on *Salix,* 27 August 1972, *D. L. Hawksworth* 3075 (IMI 168590!); S. Devon, Cornwood, Dendles Wood, on *P. laevigata,* 29 February 1976, *D. L. Hawksworth* 4293a (IMI 201661*a*). Scotland, Dumfriesshire, nr Gretna, on *P. sulcata* on *Ulmus,* 6 August 1972, *B. J. Coppins* (E!); Argyll, S side Loch Sunart, on *P. laevigata,* 14 August 1972, *S. R. Davey* (IMI 250032*b*).

3. Phoma dubia (Lindsay) Sacc. & A. Trotter, *in* Saccardo, *Syll. Fung.* **22** : 897 (1913)*. (Fig. 26A–D)

Phoma dubia* Rupprecht (*Sydowia* **11 : 128, 1958), described from *Stellaria graminea* in Hungary, is a later homonym which must be rejected under Art. 64.1.

Phymatopsis dubia Lindsay, *Trans. R. Soc. Edinb.* **24** : 442 (1866).
Type: New Zealand, Otago, Pelichet Bay, in the bush, on *Usnea* sp. (apothecia), 17 December 1861, *W. L. Lindsay* (E—holotype!).

Icones: Lindsay, *Trans. R. Soc. Edinb.* **24** : pl. 30 figs. 36–41 (1866).

Conidiomata pycnidial, immersed in the hymenium of the host, only the ostiole sometimes slightly protruding above the level of the epithecium, scattered to loosely aggregated, sometimes almost confluent, subglobose, 25–60 μm diam, ostiolate; wall mainly 1–3 layers of cells thick, mostly 3·5–5 μm thick but to 8 μm near the ostiole, cells pseudoparenchymatous, subglobose to somewhat polyhedral, subhyaline except in the vicinity of the ostiole and there thicker-walled and golden-brown, mainly 2–3 μm diam. *Conidiogenous cells* arising from the inner wall of the pycnidium, short-ampulliform to obpyriform, hyaline, smooth-walled, phialidic, not proliferating, 4–8 × 3–5 μm. *Conidia* abundant, narrowly ellipsoid to almost bacilliform, sometimes slightly truncated at the base, hyaline, simple, 0–2 guttulate, smooth-walled, 3·5 × 1·5–2 μm.

Host: Usnea sp., apothecia. The host was originally named as *U. barbata* var. *florida* (L.) Fr. (i.e. *U. florida* (L.) Wigg.) by Lindsay but I am not sure that it really belongs there; certain identification must await a re-evaluation of that genus in New Zealand. The infected parts of the apothecial disc become discoloured and brownish suggesting that *Phoma dubia* is a mild pathogen.

Distribution: New Zealand. Known only from the original collection.

Observations: This fungus is clearly separated from the other lichenicolous *Phoma* species treated here by the minute conidia.

4. Phoma peltigerae (P. Karsten) D. Hawksw., *Trans. Br. mycol. Soc.* **74** : 381 (1980). (Fig. 27A–E)

Phyllosticta peltigerae P. Karsten, *Hedwigia* **23** : 62 (1884).
Type: Finland, Tavastia australis, Tammela, Kytö, on *Peltigera malacea*, 4 May 1869, *P. A. Karsten* (H-KARST 2040—holotype!).

Conidiomata pycnidial, ± completely immersed at first, the upper $\frac{1}{3}$ erumpent at maturity, arising singly, scattered, black, subglobose, (75–)100–150(–200) μm diam, ostiolate, cells surrounding the ostiole dark brown to black and darker than the remainder of the wall; wall 1–2 layers of cells thick, 5–8 μm thick, cells pseudoparenchymatous, the outermost dark brown with the external wall thickened, not markedly radially compressed, 5–9 μm long and 4–7 μm tall, the inner cells subhyaline to pale brown and with thinner walls. *Conidiogenous cells* arising from the inner wall of the pycnidium, lining the pycnidial cavity, subglobose to broadly obpyriform, hyaline, smooth-walled, phialidic, not proliferating, 4–6 μm diam. *Conidia* abundant, narrowly ellipsoid, rounded at the apices, hyaline, simple, sometimes guttulate, smooth-walled, (4–)4·5–6(–7) × 2–2·5(–3) μm.

Host: Peltigera malacea (Ach.) Funck, thallus. The host in the type collection was originally determined as *P. canina* (L.) Willd., and this has been given as the host in all previous references to this species. On *P. malacea* the infected area becomes entirely decolourized, the whitened patches being 5–10 mm across and very sharply delimited from the healthy tissues; a slight blackening of the host occurs just at the margin of the infection spot. *Phoma peltigerae* consequently appears to be pathogenic to this species. This fungus has also been reported from *P. horizontalis* (Huds.) Baumg., *P. polydactyla* (Necker) Hoffm. and *P. rufescens* (Weis) Humb. by Vouaux (1914 : 193), and Keissler (1930 : 536) mentions a report on *Platismatia glauca* (L.) Culb. & C. Culb.; these four host records require substantiation.

Distribution: Finland. Known to me only from the type collection but mentioned as present in France by Bouly de Lesdain (1910 : 276) and Vouaux (1914 : 193), and in Germany by Keissler (1930 : 536, 1933 : 392).

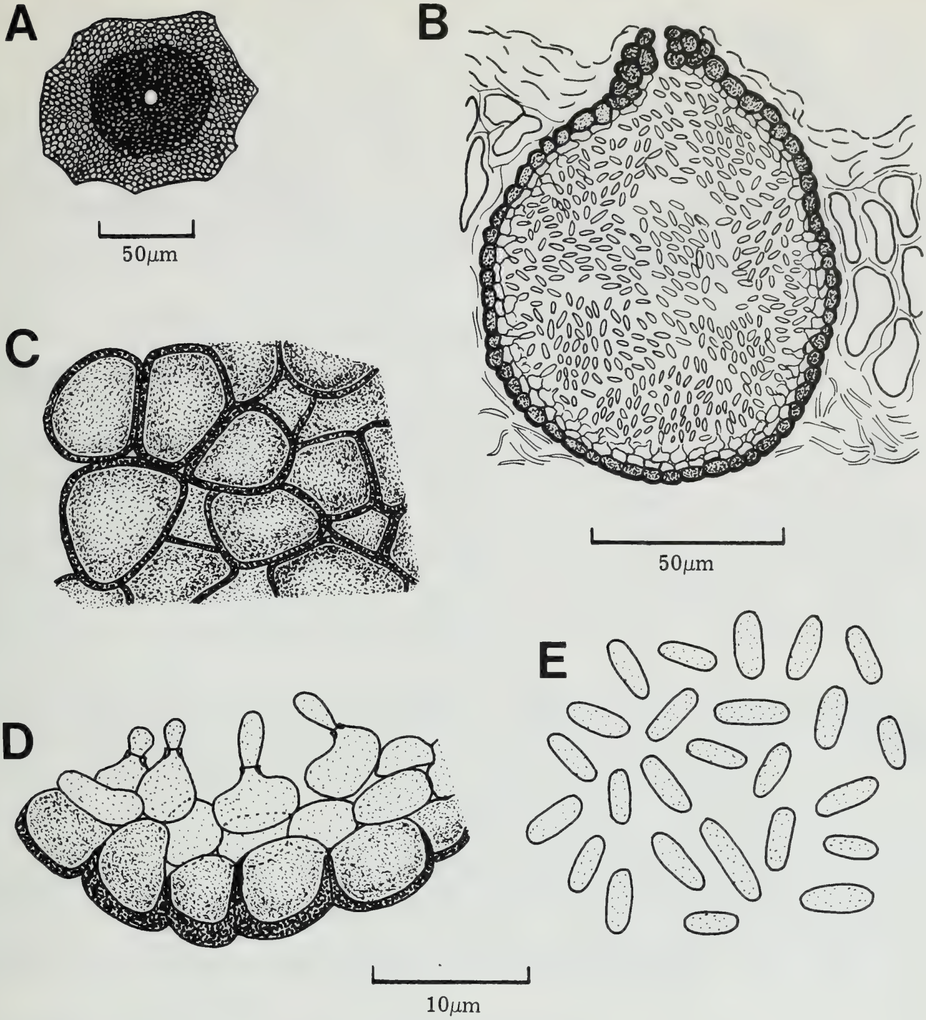

Fig. 27 *Phoma peltigerae* (H-KARST 2041—holotype). **A,** Surface view of pycnidium. **B,** Vertical section of pycnidium. **C,** Surface view of pycnidial wall. **D,** Conidiogenous cells and pycnidial wall. **E,** Conidia.

Observations: Phoma peltigerae recalls *P. cytospora* but differs in the broader conidia, thickening of the pycnidial wall cells, and larger pycnidia, as well as in occurring on quite different hosts.

Phyllosticta peltigerae was originally described from 'Mustiala' but no material under this name from that locality could be found in H-KARST (O. Vitikainen, *in litt.*). However, in a packet incorrectly labelled as '*Stagonopsis peltigerae*' in W. Nyberg's hand (an amateur mycologist who once helped in H) was a slip of paper with the herbarium name '*Phoma peltigerae*' in Karsten's writing, conidial characters and notes conforming to the published description of *Phyllosticta peltigerae,* and the locality name Kytö. This is a place name in Tammela parish, situated west of Mustiala (O. Vitikainen, *in litt.*), and it appears that when publishing this fungus Karsten (a) used a nearby better-known locality name, and (b) as *Phoma* and *Phyllosticta* were then separated according to whether the fungus was on a stem or leaf, decided that the thallus of *Peltigera* was leaf-like not stem-like. H-KARST 2040 is consequently considered to be the holotype of *Phyllosticta peltigerae.*

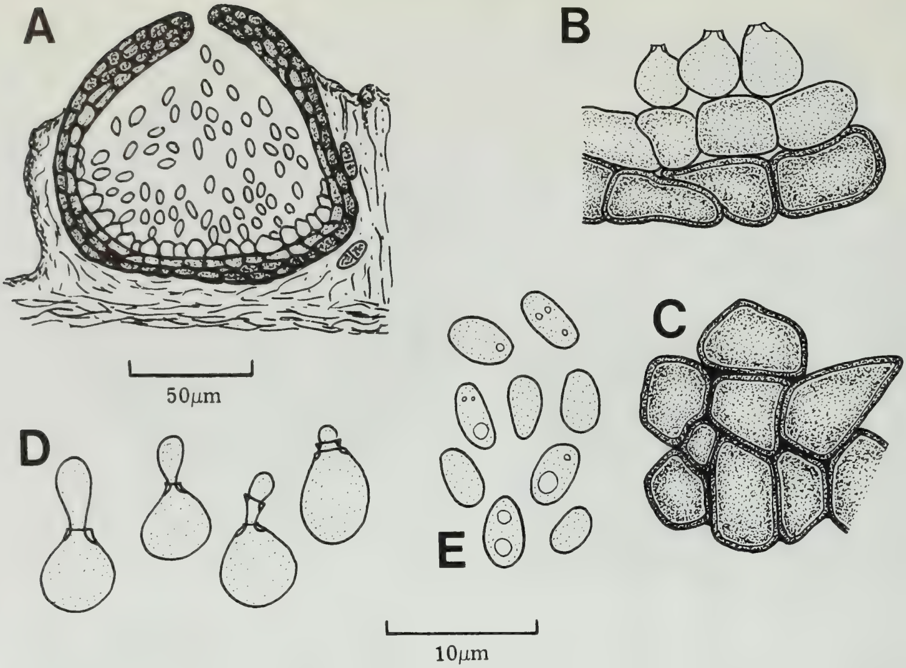

Fig. 28 *Phoma physciicola* (W 1910/609—holotype). **A**, Vertical section of pycnidium. **B**, Conidiogenous cells and pycnidial wall. **C**, Surface view of pycnidial wall. **D**, Conidigenous cells. **E**, Conidia.

5. Phoma physciicola Keissler, *Hedwigia* **50** : 294 (1911). (Fig. 28A–E)

Type: Austria, Steiermark, Gams bei Hieflau, on *Physcia aipolia*, June 1910, *K. von Keissler* (W 1910/609—holotype!).

Icones: Keissler, *Hedwigia* **50** : 295 fig. 1a-c (1911).—Keissler, *Rabenh. Krypt.-Fl.* **8** : 539 figs. 102–103 (1930).

Conidiomata pycnidial, immersed at first, with the upper $\frac{1}{3}$ erumpent at maturity, arising singly or in small groups, black, subglobose, 100–150 μm diam, ostiolate, cells surrounding the ostiole dark brown to black and darker than the remainder of the wall; wall 1–3 layers of cells thick, mainly 7–10 μm thick but to 15 μm near the ostiole, cells pseudoparenchymatous, the outermost brown with moderately thickened walls, not markedly radially compressed, 5–7 μm diam in side view, 5–10 μm diam and rather angular in surface view, the inner cells pale brown to subhyaline and with thinner walls. *Conidiogenous cells* arising from the inner wall of the pycnidium, lining the pycnidial cavity, subglobose, hyaline, smooth-walled, phialidic, very rarely proliferating, 4–7 μm diam. *Conidia* abundant, broadly ellipsoid, rounded at the apices, hyaline, simple, frequently with 2 or more guttules, smooth-walled, 4–5·5(–6) × 2·5–3·5(–4) μm.

Host: Physcia aipolia (Humb.) Fürnrohr and *Physconia pulverulacea* Moberg, apothecia. Also cited by Keissler (1930 : 542) from *Baeomyces rufus* (Huds.) Rebent. (thallus), *Parmelia caperata* (L.) Ach. (thallus) and *P. glabratula* (Lamy) Nyl. (thallus) but these reports are dubious and require confirmation. In the holotype, as many as 15 pycnidia may occur in a single apothecium of the host in which they are rather strictly confined to the thecium, scarcely extending down into the hypothecium. Infected apothecia retain their black colour but lose their characteristic whitish pruina; ascospores still formed in the most heavily infected apothecia studied.

Distribution: Austria and Sweden.

Observations: Phoma physciicola is separated from other species of the genus accepted here by the shape and size of the conidia. *Phoma caperatae* Vouaux was treated first as a variety of *P. physciicola* and later subsumed under this species by Keissler (1930 : 542), but it is most unlikely that these taxa are conspecific (see p. 80).

Additional specimens: **Sweden:** Småland, Aneboda s:n, Aneboda limnologiska laboratorium, på lönn, i allé, on *Physconia pulverulacea,* 27 July 1947, *R. Santesson* (UPS!); Södermanland, Bankyska s:n, Sturehav, allé träd, on *P. pulverulacea,* 21 July 1944, *R. Santesson* (UPS!).

XVII. PSEUDOSEPTORIA Speg.

An. Mus. nac. B. Aires **20 :** 388 (1910).
Lunospora Frandsen, *Meddr Kgl. Veter. Landboh. Kobenh.* **26 :** 70 (1943).

Conidiomata pycnidial, arising singly or aggregated into short rows, globose, immersed to erumpent, brown to black, ostiolate; walls composed of a few layers of cells, cells pseudoparenchymatous, thin- to moderately thick-walled, pale to greenish or dark brown, textura angularis. *Conidiophores* absent. *Conidiogenous cells* holoblastic, lining the inner wall of the pycnidial cavity, acrogenous or sympodial, subcylindrical to ampulliform, often proliferating, then with distinct annellations, hyaline. *Conidia* not catenate, falcate, fusiform or cymbiform, attenuated at the apex, attenuated to truncate at the base, hyaline, simple, smooth-walled.

Type species: Pseudoseptoria donacis (Pass.) B. Sutton (syn. *P. donacicola* Speg.).

Number of species: Four species are treated by Sutton (1980), all of which are graminicolous. A fifth lichenicolous species is added to the genus here.

Observations: The genus *Pseudoseptoria* has been revived by Sutton (1980) for several graminicolous species hitherto referred to *Selenophoma* Maire, a genus that differs in both pycnidium structure and the method of conidiogenesis. The inclusion of *Phoma usneae* Vouaux in the genus expands the generic concept slightly to embrace species in which the conidia are not strongly falcate. It is probable that some additional non-lichenicolous and non-graminicolous will eventually be found to require transfer here.

1. Pseudoseptoria usneae (Vouaux) D. Hawksw. comb. nov.
(Fig. 29A–B)

Phoma usneae Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30 :** 196 (1914).
Type: Italy, Tirol, Bolzano [Bolzen], Mendola [Mendel], wood by Mt Roén [Roen], on *Usnea filipendula* aggr. (thallus), 13 August 1896, *F. G. C. Arnold* [*Lich. Exs.* no. 1718 p.p.] (K—isotype!).

Exsiccatae: Arnold, *Lich. Exs.* no. 1718 p.p. (K!; sub *Epicoccum usneae* Anzi).

Conidiomata pycnidial, immersed at first but becoming erumpent with age, arising singly, scattered, black, subglobose, ostiolate, 75–100(–200) μm diam when mature; wall about 3–4 layers of cells thick, cells moderately thick-walled, pseudoparenchymatous, forming a textura angularis, subglobose to polyhedral, greenish brown, 4–7 μm diam. *Conidiogenous cells* holoblastic, lining the inner wall of the pycnidial cavity, subcylindrical to ampulliform, percurrently proliferating, to 4 annellations seen, hyaline, smooth-walled, rarely proliferating sympodially, 6–12 × 3–5 μm. *Conidia* cymbiform, tapering to the rounded apex but with an abruptly truncated base, base 2–3 μm wide, hyaline, smooth-walled, simple, often with numerous small guttules, (10–)12–14(–16) × (3–)3·5–4 μm.

Host: Usnea filipendula Stirton aggr., thallus. The fungus is present on some of the smaller branches but very few pycnidia were found on the isotype studied. Infection, at least in its early stages, does not appear to damage the host significantly. The apothecia in the type

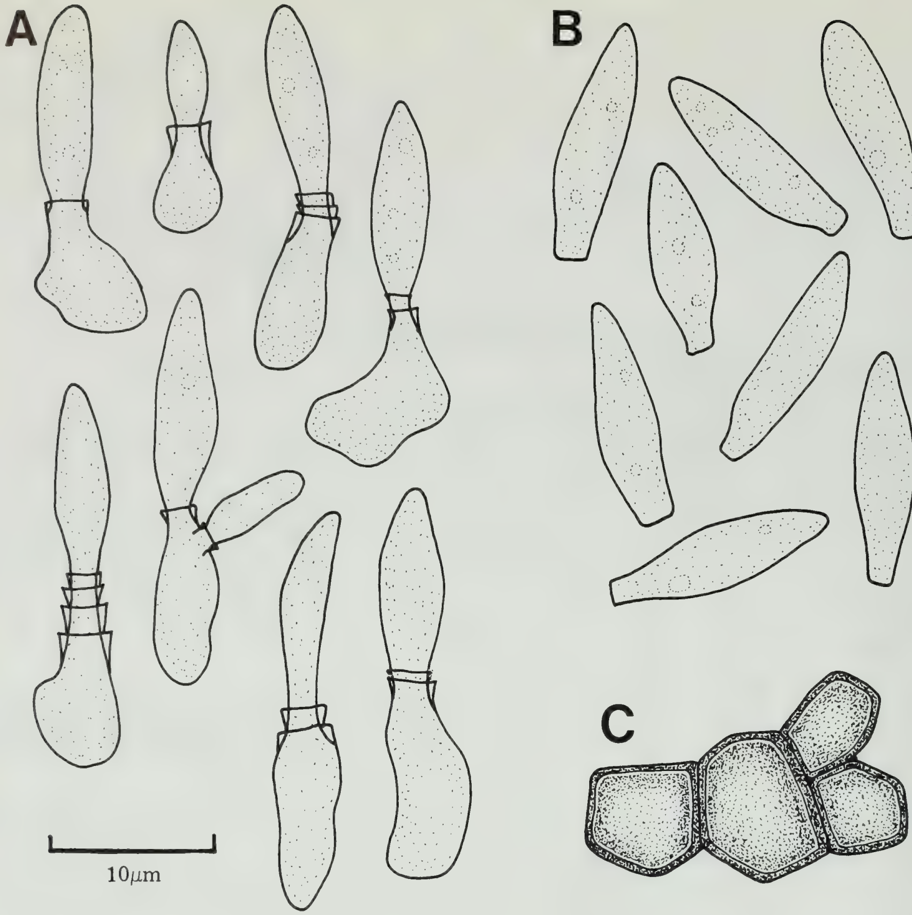

Fig. 29 *Pseudoseptoria usneae* (K—isotype). **A,** Conidiogenous cells. **B,** Conidia. **C,** Surface view of cells of pycnidial wall.

collection are infected with *Lichenoconium usneae* (Anzi) D. Hawksw., and some dark brown torulose mycelium and galls that may be young *Abrothallus usneae* Rabenh. are present on other parts of the thallus.

Distribution: Italy and Spain (*fide* Santesson, 1960 : 519).

Observations: Vouaux described this taxon on the basis of the example of Arnold's exsiccatum in Harmand's herbarium. This could not be located amongst Harmand's herbarium in Angers (M. Guerlesquin, *in litt.*) but one collection of this number in K was found to have a few pycnidia producing conidia conforming so precisely to Vouaux's description that there can be no doubt they belong to the same fungus. The only discrepancies noted were that Vouaux indicated the pycnidia were 100–200 μm diam and that he gave the conidiogenous cells as only 3–6 × 2 μm. So few pycnidia were present on the specimen in K that no microtome sections were prepared; a more detailed account of the pycnidium structure must consequently await the availability of further material of this taxon.

This species occupies a rather isolated position in *Pseudoseptoria* as currently circumscribed in view of the relatively broad and ± straight, rather than curved or falcate, conidia. Such a difference scarcely merits a generic separation, however, as it seem to agree with the type species of the genus in all other details.

Keissler (1960 : 416) indicated that this fungus could be distinguished from the normal pycnidia of *Usnea* species in that the conidiogenous cells were simple, but there are many other differences also. For example, the conidia of *Usnea* are, contrary to some earlier reports, bacillariform with a marked swelling just above the base so that they appear pendulum-shaped (Swinscow & Krog, 1976 : 264–5).

XVIII. **PYRENOTRICHUM** Mont.

Annls Sci. nat. (Bot.) II **20** : 376 (1843).
Chlorocyphella Speg., *An. Mus. nac. B. Aires* **19** : 279 (1909).

Conidiomata ('campylidia', 'orthidia') helmet-shaped, erect, convoluted or becoming adpressed, superficial, arising singly, not aggregated into stromata, pale fawn to shades of blue-green or blue-black, wall thick at the base but tapering towards the tip, outer convex surface composed of arachnoid hyphae, central tissue and inner concave surface of hyaline to pigmented thick-walled pseudoparenchymatous cells, textura angularis. *Conidiophores* mainly in the lower part of the concave surface, simple or branched near the base, septate or unicellular, conidiogenous cells arising at ± the same level, ellipsoid to subcylindrical. *Conidiogenous cells* probably enteroblastic, phialidic, not proliferating, lacking distinct collarettes, hyaline, smooth-walled, subcylindrical. *Conidia* arising singly, ellipsoid, pyriform, clavate, filiform or scolecosporous, sometimes variously curved, 0-multiseptate, not or distinctly branched, hyaline, smooth-walled.

Type species: Pyrenotrichum splitgerberi Mont.

Number of species: Three species have validly published names in *Pyrenotrichum,* and Santesson (1952 : 41) recognized six additional species which have not yet been formally published. All these nine species are parasymbionts on tropical foliicolous lichens and it is probable that there are additional species awaiting description on other crustose lichens on bark in the tropics (see below).

Observations: Pyrenotrichum species are evidently widespread in the tropics and have been studied in some detail by Santesson; unfortunately only a brief account of his important investigations has so far appeared (Santesson, 1952 : 40–41). I have not attempted to duplicate his research and consequently describe in full only the type species of the genus and note one of the other species with a validly published name represented in IMI. In addition to these two species, *P. foliicola* mentioned under *P. staurosporum*, and *P. filiferum* mentioned under *P. splitgerberi,* Santesson accepts five species with simple or 1-septate conidia; ellipsoid conidia occur in *P. bicolor* R. Sant. *ined.* (on *Lopadium flammeum* Müll. Arg.), *P. mirum* R. Sant. *ined.* (on *L. tayabasense* (Vainio) Zahlbr.), and *P. atrocyaneum* R. Sant. *ined.* (on *Lopadium* sp.); and ± pyriform to ± clavate conidia in *P. irregulare* R. Sant. *ined.* (on four *Sporopodium* species), and *P. podosphaera* R. Sant. *ined* (on *Sporopodium* sp.).

The genus is evidently not restricted to foliicolous lichens as I have seen two collections referrable to it on sterile crustose lichens on bark from the tropics (**Ecuador:** Galapagos Island, Isla Pinta, near volcano in south-central part, on *Tournefortia* sp., 8 July 1976, *H. Sipman,* COLO-L63608, IMI 214571!; **St Helena:** Ascension Island, Green Mountain, nr summit, on *Podocarpus* sp. bark, 30 October 1976, *P. W. James,* IMI 251280!). Whether these represent additional new species is unclear, resultant upon the publication of Santesson's revision.

It is possible that some of the allegedly lichenized foliicolous Coelomycetes described by Brazilian workers in recent years also belong to *Pyrenotrichum* as interpreted by Santesson, for example *Acleistomyces rionegrensis* Bat. & Maia with ellipsoid, simple, conidia (Batista, 1961). The status of many of the taxa introduced by these workers requires a critical re-evaluation; the generic names involved are compiled by Vobis & Hawksworth (1981).

Keissler (1927 : 159) listed generic names '*Campylidium* Müll. Arg.' and '*Orthidium* Müll. Arg.' as synonyms of *Chlorocyphella;* this is quite incorrect as Müller (1881 : 111,

1890 : 202) introduced these as anatomical terms for conidiomata of different shapes and *not* as generic names. Neither of these names is validly published as a genus.

I found the method of conidiogenesis in *P. splitgerberi* difficult to ascertain conclusively, even by differential interference contrast. Although the conidia are often large, at the point of secession a structure only about 1·5 μm wide must be resolved; ultrastructural studies will be necessary to conclusively determine this matter.

Key to the species treated

1 Conidia unbranched, filiform, multi-septate, arcuate to C- or S-shaped or variously convoluted, 55–80 × 2–3 μm . . . . **Pyrenotrichum splitgerberi** (p. 60)

– Conidia with a main stem and 2–4 branches arising at a single locus about half way along the conidum, arms at acute angles, straight to slightly flexous, 60–85 × 2·5–3·5 μm . . . **Pyrenotrichum staurosporum** (p. 63)

1. Pyrenotrichum splitgerberi Mont., *Annls Sci. nat.* (Bot.) II, **20** : 377 (1843). (Figs. 30A–F, 31A–B)

Lecidea irregularis Fée, *Bull. Soc. bot. Fr.* **20** : 318 (1873).
Melophia woodsiana Sacc. & Berl., *in* Saccardo, *Syll. Fung.* **3** : 659 (1884)*.
Cyphella subcyanea Ell. & Ev., *J. Mycol.* **2** : 37 (1886).
Cyphella aeruginascens P. Karsten, *Hedwigia* **28** : 191 (1889).
Chlorocyphella aeruginascens (P. Karsten) Keissler, *Annln naturh. Mus. Wien* **41** : 159 (1927).
? *Trichosperma cyphelloidea* Höhnel, *Sber. Akad. Wiss. Wien* I, **116** : 145 (1907)*.
?*Trichosperma aeruginosa* Höhnel, *Sber. Akad. Wiss. Wien* I, **118** : 1530 (1909)*.
Chlorocyphella subtropica Speg., *An. Mus. nac. B. Aires* **19** : 279 (1909).
Chlorocyphella aeruginascens var. *convoluta* Keissler, *Annln naturh. Mus. Wien* **41** : 161 (1927).
Chlorocyphella lichenicola Keissler, *in* Zahlbruckner *et al., Trans. Proc. N.Z. Inst.* **59** : 313 (1928).

Icones: Keissler, *Annln naturh. Mus. Wien* **41** : 161 fig. 1*a-b* (1927).—Mameli-Calvino, *Nuovo G. bot. ital.* II, **37** : pl. 19 figs. 1–16 (1930).—Montagne, *Annls Sci. nat.* (Bot.) II, **20** : pl. 16 fig. 2*a–m* (1843).—Rizzini, *Archos Jard. bot., Rio de J.* **12** : figs. 1–7 (1952).

Conidiomata helmet-shaped, ± erect, convoluted, or geniculately adpressed, entirely superficial, almost fawn to blue-green or blue-black, mat, arising singly, scattered, often rather evenly and sparsely distributed over the host thallus, very variable in size and shape, mainly 300–800 μm long and 250–600 μm wide when mature; wall 40–60 μm thick at the base but tapering to about 10 μm thick at the tip, in vertical section seen to be composed of two layers, an irregular outer layer of arachnoidly branched thick-walled hyphae 3–3·5 μm wide with granular incrustations often evident on their walls, and air-spaces present in the gaps formed by the hyphae, inner layer of thick-walled pseudoparenchymatous cells, textura angularis, cells irregularly subglobose to ellipsoid or polyhedral, mainly 4–9 μm diam, without air spaces, subhyaline to olivaceous, the cells towards the inner concave side adjacent to the conidiogenous layer most deeply pigmented, those above the conidiogenous region often with papilliform projections. *Conidiophores* simple or branched near the base, septate or unicellular, hyaline, ellipsoid to subcylindrical, with 1–3 conidiogenous cells arising at about the same level, to 10 × 3 μm, restricted to the concave surface of the conidiomata and not extending more than about $\frac{1}{3}$ of the length of the conidiomata in the specimens sectioned. *Conidiogenous cells* probably enteroblastic, phialidic with minute apical thickenings, arising from the conidiophores or sometimes apparently directly from the innermost wall cells, hyaline, smooth-walled, subcylindrical, slightly wider at the base but not ampulliform, mainly 10–12 × 2·5–3·5(–4) μm. *Conidia* abundantly produced, arising singly, filiform, scolecosporous, arcuate to C- or S-shaped or

*Santesson (1952 : 52) attributes combinations of these three epithets into *Pyrenotrichum* to Höhnel; Höhnel (1910 : 652) suggested these species should be placed in that genus but did not validly publish the transfers (they were also not accepted in his 'Index', *loc. cit.:* 678).

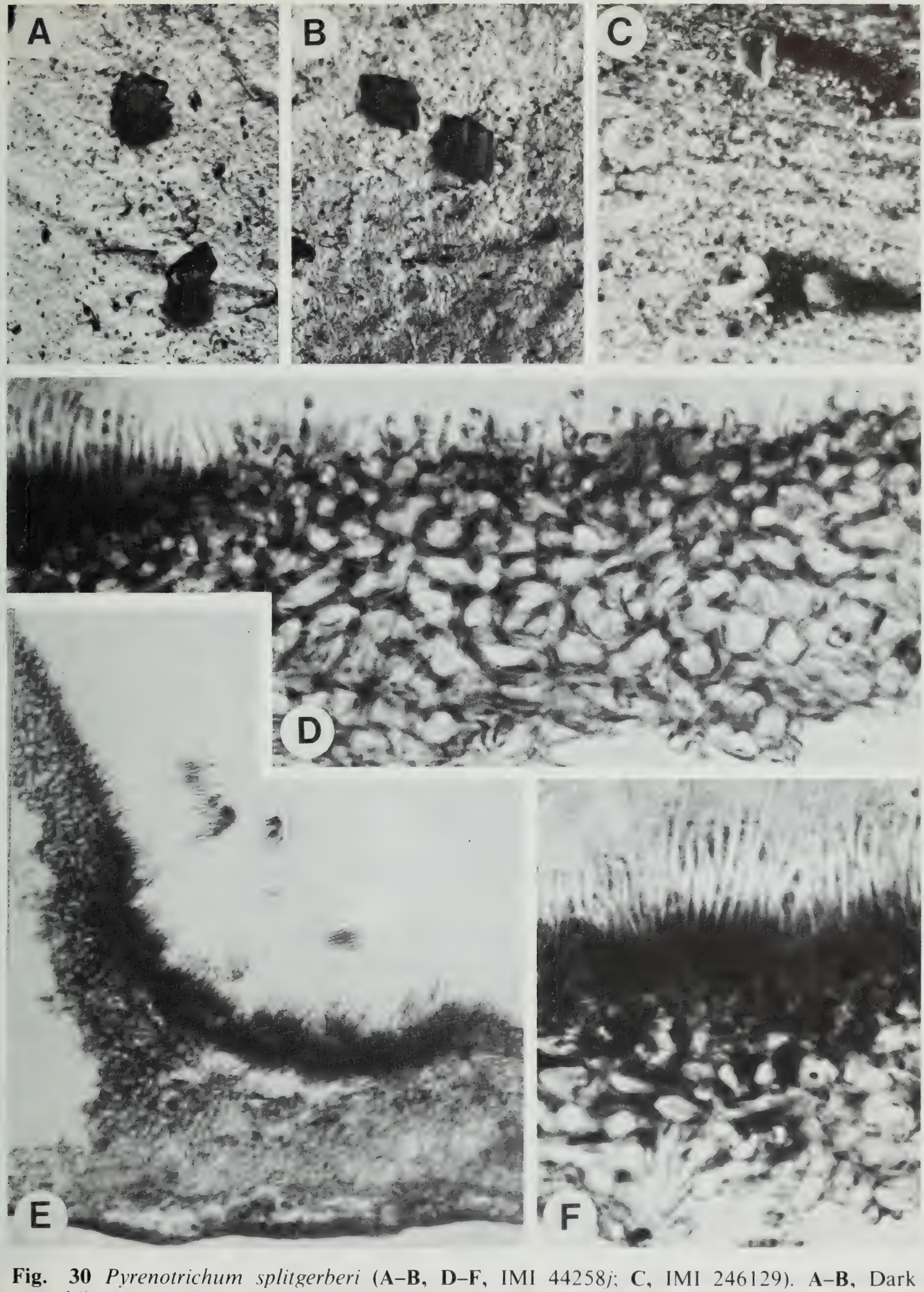

Fig. 30 *Pyrenotrichum splitgerberi* (**A–B**, **D–F**, IMI 44258*j*; **C**, IMI 246129). **A–B**, Dark conidiomata (× 16). **C**, Light conidiomata (× 25). **D**, Vertical section of conidoma showing portion with conidiogenous cells (left) and papillae not bearing conidia (centre to right) (× 1020). **E**, Vertical section of conidioma (× 250). **F**, Vertical section of lower part of conidioma showing the branched conidiophores (× 1020).

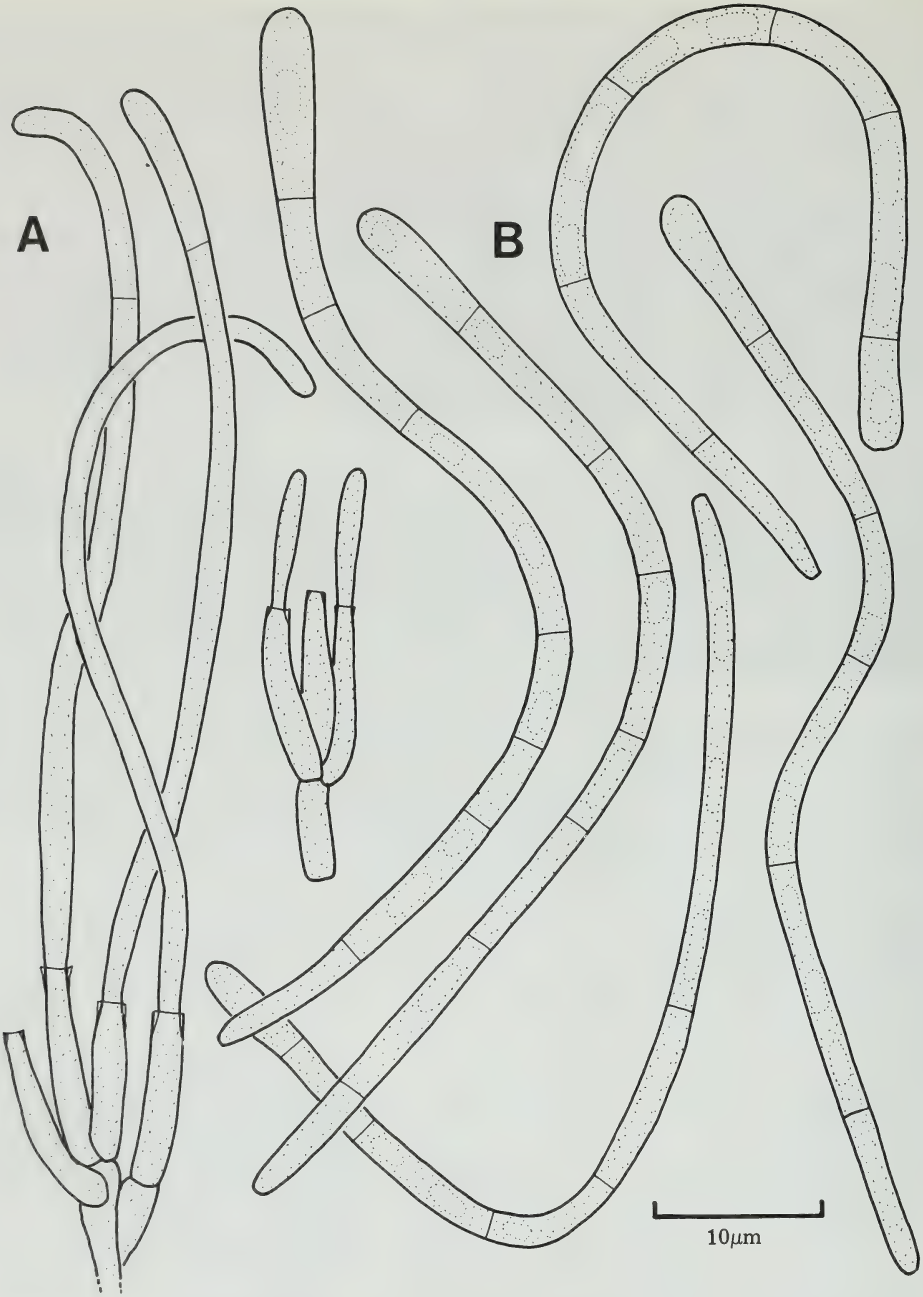

Fig. 31 *Pyrenotrichum splitgerberi* (IMI 44258*j*). **A,** Conidiophores, conidiogenous cells and developing conidia. **B,** Conidia.

otherwise convoluted, slightly thicker at the rounded apex, truncated and to about 1 μm wide at the extreme base, hyaline, multiseptate, with to 8 septa when mature, often with numerous guttules, smooth-walled, 55–80 × 2–3 μm.

Hosts: According to Santesson (1952 : 40) this species is restricted to the thalli of foliicolous lichens belong to the genera *Lopadium* Körber (9 species) and *Tapellaria* Müll. Arg. (6 species). Parasymbiotic, sometimes apparently depressing the formation of apothecia

in the host and then appearing as if a lichen-forming coelomycete. This species has been considered to be a lichen by several authors (e.g. Mameli-Calvino, 1930; Rizzini, 1952) and it may be that in some cases the fungus can take over the algae from the original lichen thallus it invades, so becoming lichenized (cf. *Blarneya hibernica* D. Hawksw. *et al.*; Hawksworth *et al.*, 1980). A critical anatomical investigation of the fungus-alga relationship in material of this species on 'sterile' thalli lacking apothecia would be of interest.

Distribution: Probably pantropical. There are reliable reports at least from Brazil, China, Cuba, Ghana, New Zealand, Surinam, and the U.S.A. (Louisiana).

Observations: I have not carried out a critical investigation into the range of variation of this species in view of Santesson's unpublished studies; the above description is mainly based on IMI 44258*j* (determined by Santesson in 1951). The synonymy presented above is derived from Keissler (1927, 1933), Santesson (1952 : 49–53), and a few minor sources; I have not studied any of the relevant type collections. Santesson (1952 : 41) mentions only one other species of the genus as having ± filiform unbranched and multiseptate conidia, *P. filiferum* R. Sant. *ined.*, known from two species of *Lopadium;* the characters separating this species from *P. splitgerberi* were not indicated.

Specimens: **Brazil:** Rio de Janeiro, Jardin Botanico, on *Buxus sempivirens,* 1947, *C. T. Rizzini 11* (PC!); Paraná, Desvio Ypiranga, 26 September 1909, *P. Dusén* 8822 (PC!); *sine loc.,* comm. March 1951, comm. R. Santesson (IMI 45098!).—**Ghana:** Pokoasi, on *Diospyros* sp., 1 June 1949, *S. J. Hughes* 1040 (IMI 43725*c*); *loc. cit.,* on *Lopadium* sp. on *Pancovia bijuga,* 25 May 1949, *S. J. Hughes* 834 (IMI 44258j!); Aburi, on *Trycalysia* cf. *pallens*, 24 May 1949, *S. J. Hughes* 807 (IMI 44170d!); near Nsuaem, 8 May 1949, *S. J. Hughes* 219 (IMI 44219*b*!); Togoland, Jasikan, on *Cola caricifolia,* 27 May 1949, *S. J. Hughes* 957 (IMI 43662g!); Togoland, Hobae, on *Culcasia scandens,* 28 May 1949, *S. J. Hughes* 934b (IMI 44213a!).—**U.S.A.:** Louisiana, Assumption Parish, 2·3 mls W of Grand Bayou, on *Sabal palmetto,* 8 February 1976, *S. C. Tucker* 15448 (IMI 246129!).

2. Pyrenotrichum staurosporum (Keissler) R. Sant., *Symb. bot. upsal.* **12**(1) : 41 (1952). (Fig. 32A–B)

Chlorocyphella aeruginascens var. *staurospora* Keissler, *Annln naturh. Mus. Wien* **41** : 162 (1927).

Icones: Keissler, *Annln naturh. Mus. Wien* **41** : 161 fig. 1*c* (1927).

This fungus is very similar in habit to *Pyrenotrichum splitgerberi* but is clearly separated from that species in that the conidia are branched with 2–4 arms arising at a single locus from a point about half way along the total length of the conidium. In the specimens studied, the conidia were (overall) 60–85 × 2·5–3·5 μm.

Hosts: According to Santesson (1952 : 40) this species is restricted to foliicolous lichens belong to the genus *Lasioloma* R. Sant. (4 species). Parasymbiotic.

Distribution: This taxon was first described from Guam but I have seen specimens also from Ghana and Malaysia.

Observations: This species is clearly separated from *Pyrenotrichum splitgerberi* on the basis of its branched conidia as well as the disparate hosts. Santesson (1952 : 41) transferred a second species with branched conidia to *Pyrenotrichum, P. foliicola* (Vainio) R. Sant.*; this was first described from the Phillipine Islands and occurs on foliicolous species of *Bacidia* de Not. (5 listed by Santesson, *loc. cit.:* 40). I have not seen any material of *P. foliicola.* Although Santesson did not give the basionyms of *P. foliicola* nor *P. staurospoum,* his combinations are treated as validly published here as these taxa were clearly accepted as distinct, albeit in a Table. As Santessons's monograph appeared before 1 January 1953, Art. 33.2 does not apply.

Symb. bot. upsal.* **12(1) : 41 (1952).—*Cyphella foliicola* Vainio, *Annls Acad. Sci. fenn.* **15**(6) : 83 (1921).—*Chlorocyphella foliicola* (Vainio) Keissler, *Annln naturh. Mus. Wien* **41** : 159 (1927).

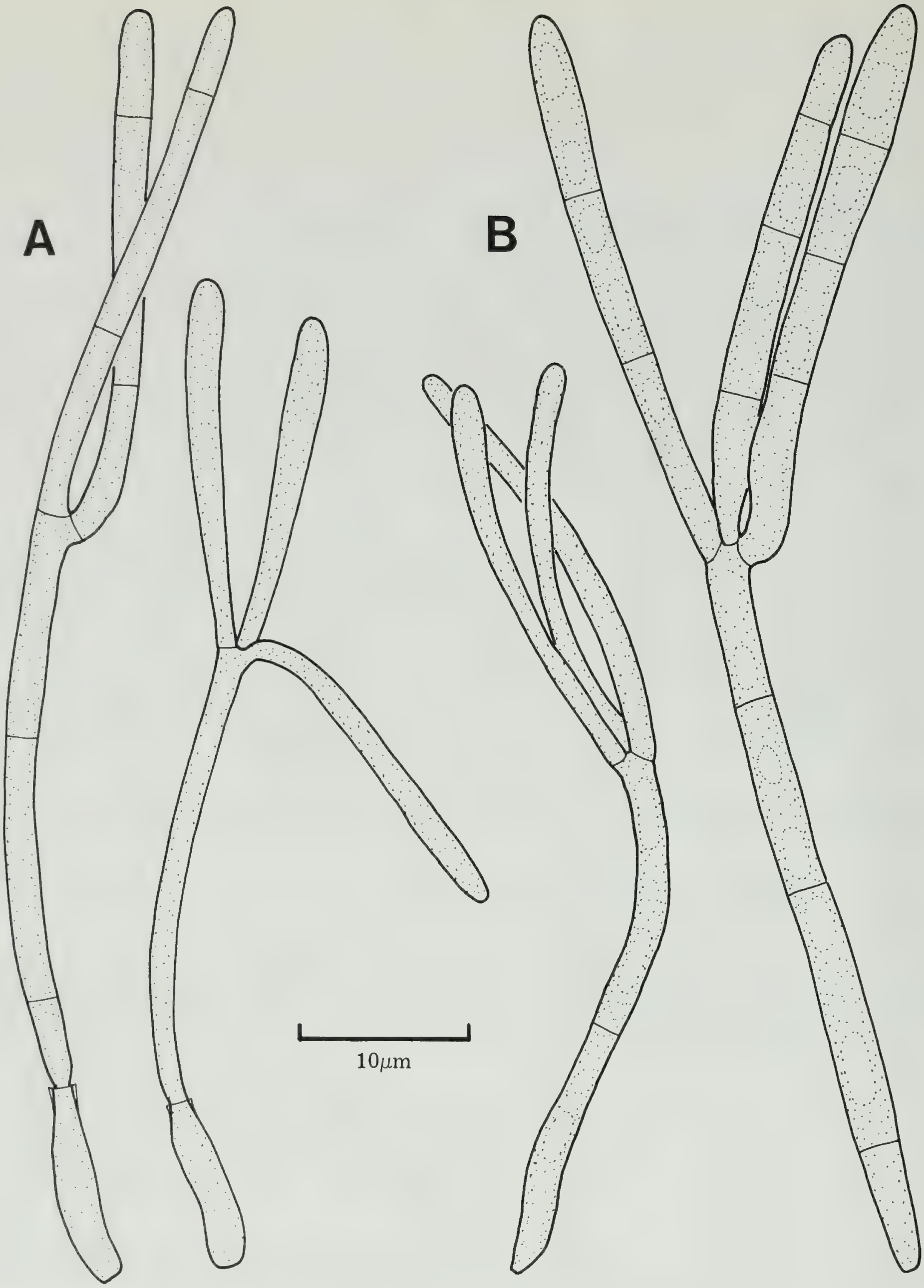

Fig. 32 *Pyrenotrichum staurosporum* (IMI 44410*d*). **A,** Conidiogenous cells and developing conidia. **B,** Conidia.

Specimens: **Ghana:** Aburi, on *Landolphia owariensis,* 24 May 1949, *S. J. Hughes* 791 (IMI 44410*d*).—**Malaysia:** Cameron Highlands, on *Lasioloma arachnoideum* on *Xanthophyllum affina,* 6 September 1953, *W. J. Cherwick* [A. Johnston no. 1113] (IMI 54915 *f–g*!).

XIX. VOUAUXIELLA Petrak & H. Sydow

Beih. Repert. nov. Spec. Regni veg. **42** : 482 (1927).

Alysia Cavalc. & Silva, *Publções Inst. Micol. Recife* **647** : 32 (1972).

Conidiomata pycnidial, arising singly, subglobose to almost cupuliform, immersed or semi-immersed, dark brown to black; walls composed of thick-walled dark brown to olivaceous green cells forming a textura angularis but sometimes almost hyphal below, the upper cells separating to form an irregularly delimited ostiole. *Conidiophores* short, branched only at the base, septate, pale brown, smooth or verruculose, lining the inner wall of the pycnidium. *Conidiogenous cells* integrated or discrete, terminal, holothallic, subhyaline to pale brown or olivaceous green, smooth or verruculose, a basal thicker-walled 'mother' cell present in some species and becoming flared at the onset of conidiogenesis. *Conidia* catenate, forming in acropetal chains, chains simple, with up to 8 or more adhering conidia, ellipsoid with both ends abruptly truncated (except in the apical conidium and in *V. uniseptata*), usually simple, rarely 1–septate, olivaceous green, brown or dark brown, smooth or verruculose, liberated by the breakup of the chains, dry.

Type species: Vouauxiella verrucosa (Vouaux) Petrak & H. Sydow (lectotype; selected by Clements & Shear, 1931 : 378).

Number of species: Four, all obligately lichenicolous, and one of which may eventually prove not to be congeneric.

Observations: Vouauxiella has an especially interesting method of conidiogenesis (Morgan-Jones, 1971; Sutton, 1980); indeed it is the only non-stromatic coelomycete with holothallic conidiogenesis recognized, with the possible exception of the new genus *Nigropuncta* described above (p. 46). As noted by Hawksworth (1978*a* : 185) and Sutton (1980 : 24), *Vouauxiella uniseptata* may well merit recognition as a distinct genus on the basis of the absence of conidiophore mother cells, much more deeply pigmented and 1-septate conidia, and the broadly opening pycnidia. *Vouauxiella* does, however, provide a convenient temporary niche for that fungus pending more detailed studies on conidiogenesis.

Key to the species

1 Conidia simple 2
– Conidia 1-septate, (10–)12–15(–17) × 5–7(–8) μm, dark brown, smooth to weakly verruculose; pycnidia almost cupuliform, 40–70 μm diam . **Vouauxiella uniseptata** (p. 66)

2 Conidia smooth-walled 3
– Conidia distinctly verruculose, 6–9 × 3·5–5 μm . . . . **Vouauxiella verrucosa** (p. 67)

3 Conidia (5–)6–8(–9) × 3–4 μm; pycnidia mainly 60–90 μm diam . . . **Vouauxiella lichenicola** (p. 65)
– Conidia 3–3·5 × 2·5μm [but see below]; pycnidia 70–160μm diam . . . **Vouauxiella pithospora** (p. 66)

1. Vouauxiella lichenicola (Lindsay) Petrak & H. Sydow, *Beih. Repert. nov. Spec. Regni veg.* **42** : 484 (1927).

This species was described and illustrated in colour in great detail by Lindsay (1869*a* : pl. 23 figs. 1–18), although he also included some other taxa in his concept. Its conidiogenesis is treated by Morgan-Jones (1971), and illustrations have been published more recently by Hawksworth (1976 : 58) and Sutton (1980 : 25). This well-known fungus is not therefore described in detail here because its diagnostic features will be apparent from the generic description and key.

The typification and synonymy of Lindsay's epithet is discussed by Hawksworth 1979 : 287).

Hosts: Lecanora species, apothecia. Especially frequent on *L. chlarotera* Nyl. but reported from a range of other red-fruited species of the genus. The pycnidia of this species and *Vouauxiella verrucosa* are characteristically found at the edges of the disc adjoining the thalline margins; infected discs are commonly paler in colour than is usual for the lichen and piebald in appearance. Reports from other host genera are dubious, partly due to confusion

with *Lichenodiplis lecanorae,* a very different fungus (p. 38), to which taxon references to it in Keissler (1930 : 568) on at least *Calopaca cerina* (Ehrh. ex Hedw.) Th. Fr., *Lecanora dispersa* (Pers.) Sommerf., and *Pertusaria leioplaca* DC., should be referred. The report of *V. lichenicola* on *Caloplaca holocarpa* (Hoffm.) Wade by Werner (1969 : 204) may also belong to that fungus.

Distribution: Probably widespread, at least in Europe. Reliably reported from the British Isles (England, Ireland, Scotland), France (Vouaux, 1914 : 297), Germany, Morocco (Werner, 1970, 1972), Spain (Santesson, 1960 : 519), Sweden (Santesson, 1949 : 143) and the U.S.A. (Mass.; Santesson, 1960 : 519). Material from Finland distributed under the name *V. lichenicola* by Räsänen (*Lich. Fenn. Exs.* no. 150, BM!) is a *Taeniolella* species.

Specimens (all on *Lecanora chlarotera* apothecia): **British Isles:** S. Devon, Slapton, Slapton Ley Nature Reserve, 30 July 1973, *D. L. Hawksworth* 3395 (IMI 178325!); *loc. cit.,* 10 October 1974, *D. L. Hawksworth* 3930 (IMI 188759!); *loc. cit.,* Peasdish, 23 August 1980, *D. L. Hawksworth* 5044c (IMI 251263!); Oxfordshire, Hook Norton, January 1973, *H. J. M. Bowen* (IMI 185887!); Sussex, Eridge Old Park, 20 May 1972, *F. Rose* (E!). Scotland, Kincardineshire, The Burn, Fettercairn, 26 July 1972, *B. J. Coppins et al.* (E!); Perthshire, Loch Tay, June 1856, *W. L. Lindsay* (E—lectotype!); E. Lothian, near Dunglass, Cockburnpath, June 1856, *J. M. Lindsay* (E!).

2. Vouauxiella pithospora (Cavalc. & Silva) B. Sutton, *The Coelomycetes*: 24 (1980).

Alysia pithospora Cavalc. & Silva, *in* Cavalcante *et al., Publções Inst. Micol. Recife* **647** : 34 (1972).

For description and illustrations see Cavalcante *et al.* (1972 : 36 fig. 7).

Host: Originally described as a lichenized coelomycete with a *Phycopeltis* phycobiont, but almost certainly a lichenicolous species on an unknown foliicolous lichen.

Distribution: Brazil (Rondonia). Known only from the original locality.

Observations: Neither Sutton (*loc. cit.*) nor myself have seen material of this taxon but the published figures leave little doubt that a species of *Vouauxiella* was involved. The pycnidia and conidia were originally given as 70–160 μm diam and 2–6 × 1·5–2·5 μm, respectively. These measurements are not in accord with the scale on the figures which suggest the pycnidia are to about 60 μm wide and the conidia 3–3·5 × 2·5 μm; these latter figures were used by Sutton. It seems impossible to resolve this discrepancy in the absence of the type material. If the scale on the figure is correct, the species is clearly separated from the others treated here by the small conidia; if the text is correct it will merit a critical comparison with *V. lichenicola.*

3. Vouauxiella uniseptata D. Hawksw., *Notes R. bot. Gdn Edinb.* **36 :** 195 (1978).

For description and illustrations see Hawksworth (1978*a* : 195–196), and Sutton (1980 : 24–25).

Host: Parmelia laevigata (Sm.) Ach., thallus. Forming distinctive raised pustular black patches, mainly 1–2 mm diam, on the lobes.

Distribution: British Isles (Scotland). Three collections were reported by Hawksworth (*loc. cit.*) and four others have since been seen (see below). Not yet seen by me on this host in Devon despite careful searches.

Observations: This species may well eventually require transfer to an independent genus for the reasons indicated above (p. 65).

Specimens (additional to those listed by Hawksworth, *loc. cit.*): **British Isles:** Scotland, Argyll, S side Loch Sunart, 14 August 1972, *S. R. Davey* (IMI 250032*a*!), Benderloch, grounds of Lochnell House, 4 August 1980, *B. J. Coppins* 8052 (E, IMI 251027!), N side Loch Etive, 8 km E of Connel Burn, 7 August 1980, *B. J. Coppins* 8083 (E, IMI 251025!); Kirkudbright, Kintyre, Tarbert, Wilhashemraig, on *Alnus,* 29 July 1973, *J. E. Menlove* (IMI 228667!).

4. Vouauxiella verrucosa (Vouaux) Petrak & H. Sydow, *Beih. Repert. nov. Spec. Regni veg.* **42** : 483 (1927).

For illustrations of this species and discussion of its separation from *V. lichenicola* see Hawksworth (1976 : 58). Further illustrations are included in Sutton (1980 : 25).

Host: Lecanora chlarotera Nyl. and *L. laevis* Poelt, apothecia and rarely thallus. The pycnidia have a similar habit to those of *Vouauxiella lichenicola* as described above and microscopic examination is therefore needed to separate these two species.

Distribution: British Isles (England, Ireland, Scotland), France and Pakistan. Perhaps often overlooked as *V. lichenicola* and perhaps much under-recorded, at least in Europe.

Observations: Lindsay (1869*a*) included material of this taxon within his concept of *V. lichenicola* but, in accordance with later usage, a smooth-spored specimen was selected as lectotype for his epithet (see above).

Specimens (additional to those listed by Hawksworth, *loc. cit.*): **British Isles:** England, Wiltshire, Imber, on *Lecanora chlarotera,* 1979, *A. M. Burnet* (IMI 237278!). Ireland, Co. Cork, near Cork, on *L. chlarotera,* March 1858, *I. Carroll* (E!).—**Pakistan:** Khanaspur, on *L. laevis,* 25 April 1975, *S. Ahmad* 1059 (IMI 199857*c*!).

XX. VOUAUXIOMYCES Dyko & D. Hawksw.

in Hawksworth & Dyko, *Lichenologist* **11** : 57 (1979).

For a description and discussion of the affinities of this genus see Hawksworth & Dyko (1979).

Type species: Vouauxiomyces truncatus (B. de Lesd.) Dyko & D. Hawksw.

Teleomorph (perfect state): Abrothallus de Not. In the course of investigations into the anamorphs of lichenicolous ascomycetes it became clear that those of *Abrothallus* were referrable to *Vouauxiomyces.* All connections are based on strong circumstantial evidence, the concurrence of ascomata and conidiomata, and have not been proved by ascospore cultures.

Number of species: Originally described as monotypic, but two additional species are added here. These three anamorphs all regularly occur without the teleomorph and it is consequently useful to have binomials available for these phases. The genus *Abrothallus* has been studied intensively by Santesson but his results still await publication; according to Santesson (*in* Nordin, 1964 : 226) the genus comprises about 15 species and it is probable that others have anamorphs in *Vouauxiomyces* also. Published accounts of anamorphs in four species of *Abrothallus* in addition to the three treated here are noted on p. 72.

Key to the species

1 Conidia exceeding 6 μm in length 2
– Conidia 3–5(–6) × 2–3·5(–4) μm; on *Ramalina* species . . **Vouauxiomyces ramalinae** (p. 67)

2(1) Conidia 6·5–8 × 4–5·5 μm; on *Parmelia caperata* and *P. perlata* . . . . **Vouauxiomyces truncatus** (p.70)
– Conidia (7–)7·5–10·5(–11·5) × (5–)5·5–7(–7·5) μm; on *Parmelia saxatilis* and *Platismatia glauca* . . . . **Vouauxiomyces santessonii** (p. 69)

1. Vouauxiomyces ramalinae (Nordin) D. Hawksw. **comb. nov.** (Fig. 33A–B)

Phoma ramalinae Nordin, *Svensk bot. Tidskr.* **58** : 227 (1964).
Type: Sweden, Uppland, Malsta par., on *Ramalina fraxinea* (L.) Ach. (apothecia), 23 May 1961, *I. Nordin* 563a (UPS—holotype n.v.).

Icones: Nordin, *Svensk bot. Tidskr.* **58** : pl. I figs 1–4, pl. II figs. 5 and 7 (1964).

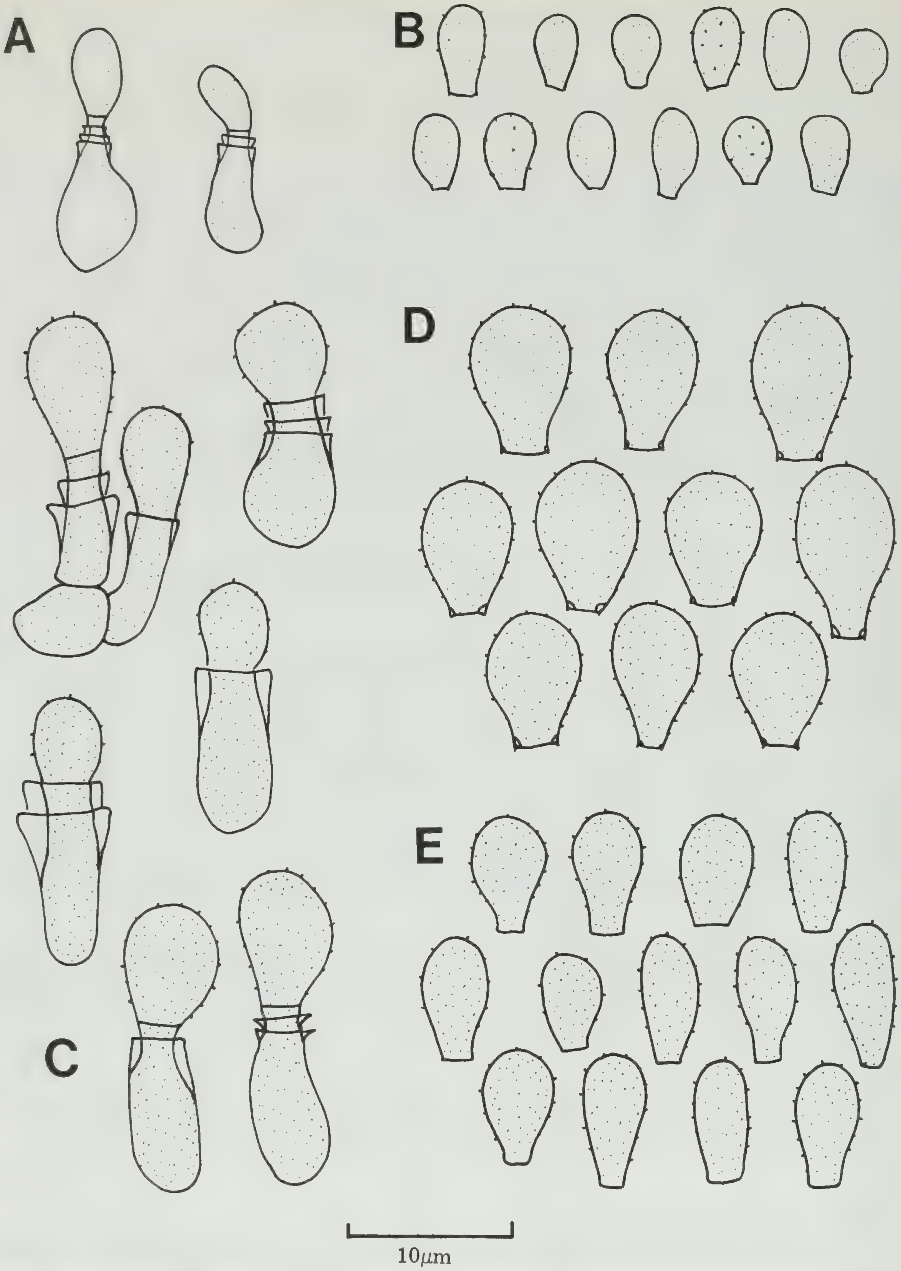

Fig. 33A–B, *Vouauxiomyces ramalinae* (IMI 194098); **A,** conidiogenous cells; **B,** conidia. **C–D,** *V. santessonii* (UPS—holotype); **C,** conidiogenous cells; **D,** conidia. **E,** *V. truncatus* (Savoie, *Santesson,* UPS), conidia.

Conidiomata pycnidial, immersed at first but becoming erumpent, to about half exposed at maturity, arising singly, scattered or sometimes in a ring in young infections, black, ostiolate, 55–75 µm diam; pycnidial wall mainly 3–5 cells thick, thickest in the exposed part adjacent to the ostiole, 5–12 µm thick, dark brown, pseudoparenchymatous, textura angularis, cells thick-walled, tending to be polyhedral, mainly 3–5 µm diam. *Conidiogenous cells* holoblastic, ampulliform to lageniform, lining the pycnidial cavity,

percurrently proliferating, to 3 annellations seen, hyaline, smooth-walled (4–)6–10 × 3–5 μm. *Conidia* arising singly, obpyriform, hyaline, collecting in a mucilaginous mass in the pycnidial cavity and extruded as a drop, simple, irregularly guttulate, apex rounded, the base abruptly truncate, ± smooth-walled by light microscopy but indications of a sparse perhaps echinulate ornamation are sometimes visible by interference contrast, 3–5(–6) × 2–3·5(–4) μm.

Teleomorph (perfect state): Abrothallus suecicus (Kirschst.) Nordin. The connection is based on the repeated occurrence of the ascomata in assocation with the anamorph.

Hosts: Ramalina calicaris (L.) Fr., *R. dilacerata* (Hoffm.) Hoffm., *R. fastigiata* (Pers.) Ach. and *R. fraxinea* (L.) Ach., thallus and especially apothecia. These hosts are taken from Nordin (1964 : 228–229) who also indicated that the species might well be present on *R. sinensis* Jatta. The symptoms and course of infection were studied carefully by Nordin, who found the pycnidia to start at one point near the margin of an apothecial disc and then extend over the disc forming pycnidia concentrically, the discs become greyish and the surface layers extremely brittle.

Distribution: British Isles (England, Ireland, Scotland), France, Finland, Norway and Sweden. Nordin (1964) reported *Abrothallus suecicus* from 104 localities, 50 of these as the anamorph alone. Evidently widespread where the host lichens are well-developed.

Observations: Vouauxiomyces ramalinae is distinguished from the other species of the genus accepted here by the smaller pycnidia, the shorter and narrower conidia, and in being associated with a different teleomorph. As the pycnidia are not uncommonly found without the ascomata, it is clearly desirable that the anamorph should have its own binomial; Nordin's epithet is consequently recombined into *Vouauxiomyces* here. The anamorph cannot be accommodated in *Phoma,* as currently circumscribed, because the conidiogenous cells are holoblastic and annellate and the conidia are not regularly bacilliform, ellipsoid or subglobose.

Specimens (see Nordin, 1964 : 229–230 for numerous other specimens he studied): **British Isles:** England, S. Devon, Slapton, Duck Marsh, on *Ramalina fastigiata* on *Salix,* 21 May 1975, *D. L. Hawksworth* 4137 (IMI 194098!). Ireland, Co. Galway, Connemara, Kilkieran, Flannery Bridge, on *R. fastigiata,* 7 August 1966, *G. Morgan-Jones* (IMI 121442*b*!).

2. Vouauxiomyces santessonii D. Hawksw. **sp. nov.**
(Fig. 33C–D)

Similis *Vouauxiomycei truncato* (B. de Lesd.) Dyko & D. Hawksw. sed differt in conidiis latioribus, (7–) 7·5–10·5(–11·5) × (5–) 5·5–7 (–7·5) μm.

Typus: Suecica, Uppland, Alsike s:n, Lunsen, vid åkertegen SV om Hjortronmossen, på grenar på marken i granskog, in thallo *Platismatiae glaucae* (L.) Culb. & C. Culb., 23. ix. 1947, *R. Santesson* (UPS—holotypus!).

Icones: Kotte, *Zentralbl. Bakt. ParasitKde* II, **24** : pl. 3 fig. 32 (1909).—Lindsay, *Q. Jl microsc. Sci.* II, **7** : pl. 5 figs. 5–7 (1857).—Schaechtelin & Werner, *Bull. trimest. Soc. mycol. Fr.* **42** : pl. 3 figs. 11–12 (1926).

Conidiomata pycnidial, immersed at first but becoming erumpent through the surface of the host, about $\frac{1}{3}$ exposed at maturity, arising singly, scattered, sometimes arising on the site of a previous pycnidium and then assuming a rimmed appearance from above and a double-walled structure in vertical section, black, ostiolate, the ostiole often conspicuous and *c.* 25 μm diam, 125–225 μm diam; wall of varying numbers of cell layers, mainly 4–8, 15–25 μm thick, thickest around the ostiole in the erumpent part of the pycnidium, dark brown, pseudoparenchymatous, textura angularis, cells thick-walled, tending to be polyhedral, mainly 3–4 μm diam. *Conidiogenous cells* holoblastic, ampulliform to lageniform, lining the pycnidial cavity, percurrently proliferating, annellate with to 4 annellations seen, hyaline, smooth-walled to weakly echinulate, 8–12 × 3–4 μm. *Conidia* obpyriform, hyaline,

collecting in a mucilaginous mass in the pycnidial cavity and extruded as a drop, simple, sometimes 1–3 guttulate, apex rounded, the base abruptly truncated, thin-walled, ± smooth-walled at lower magnifications but with a widely spaced echinulate ornamentation just discernible by interference contrast, (7–)7·5–10·5(–11·5) × (5–)5·5–7(–7·5) μm.

Teleomorph (perfect state): Abrothallus parmeliarum (Sommerf.) Arnold. The conidia of this species were well-described in some of the earliest papers on lichenicolous fungi, notably those of Tulasne (1852 : 114*) and Lindsay (1857*), and the connection has been accepted by subsequent students of *Abrothallus* (e.g. Kotte, 1909 : 87; Schaechtelin & Werner, 1926 : 238–239).

Hosts: Parmelia saxatilis (L.) Ach. and *Platismatia glauca* (L.) Culb. & C. Culb., thalli. The teleomorph is reported from a large number of species of *Parmelia,* many of which must also support the anamorph. In early infections the pycnidia arise on almost healthy lobes, with a circle of brownish discoloured tissue around the pycnidia (rarely over 25 μm thick). In more advanced stages of infection the pycnidia occur on gall-like deformations of the host thalli typical of infections due to *Abrothallus parmeliarum.*

Distribution: I have studied material of the anamorph from the British Isles and Sweden, but it can be expected to occur throughout the range of the teleomorph. The distribution of the teleomorph is difficult to ascertain from the literature due to taxonomic uncertainties but *Abrothallus parmeliarum* s. lat., in addition to being widespread in Europe, is mentioned from at least Canada, Chile, Bolivia, Ecuador, Hawaii, Tenerife, Kenya, Tasmania, Morocco, New Zealand, South Africa, Mongolia, the U.S.A., Siberia and Venezuela (Hertel, 1971 : 228–229).

Observations: This species differs from *Vouauxiomyces truncatus* in the broader, and often also longer, conidia; the taxonomic importance of this difference is substantiated by the different teleomorphs and host ranges.

The species is named in honour of Prof. Dr R. Santesson in recognition of his important, yet unpublished, studies on *Abrothallus, Pyrenotrichum,* and other lichenicolous fungi.

The name *Epicoccum parmeliarum* H. Olivier may provide an earlier epithet for this species but is not taken up here in view of some uncertainties surrounding its application (see p. 76).

Additional specimens: **British Isles:** Scotland, Argyll, 4 km E of Dalmally, wood on N side of River Lochy, on *Parmelia saxatilis* on *Quercus,* 1 August 1980, *P. W. James & B. J. Coppins* 4961 (E, IMI 251031!). Wales, Montgomery, Gregynog Hall, on *P. saxatilis* on *Fagus sylvatica,* 25 May 1979, *K. L. Brady* (IMI 239067!).—**Sweden** (all on *Platismatia glauca*): Uppland, Vänge s:n, Fiby urskog (S om Fibysjön), i granskogen Ö om Getryggen, på grankvistar, 28 April 1948, *R. Santesson* 4859 (UPS!); Viksta s:n, Djupdalen, *c.* ½ km V om Nyboda, på gran i tät barrskog, 21 May 1947, *R. Santesson* (UPS!); Rasbo parish, *c.* 1 km SSE of the lake Rokarn, on twigs of *Picea abies* in a rather dark forest, 23 October 1955, *R. Santesson* 11139b (UPS!); Skuttunge, Norra myren, 3 May 1939, *R. Sernander* (UPS!); Uppsala, Vänge socken, Fiby urskog, 15 November 1945, *B. H. Svenonius* (UPS!). Västergötland, Halleberg, Vänersnäs s:n, Hallesnipan, på ek, 15 June 1944, *R. Santesson* (UPS!).

3. Vouauxiomyces truncatus (B. de Lesd.) Dyko & D. Hawksw., *in* Hawksworth & Dyko, *Lichenologist* **11** : 58 (1979).
(Fig. 33E, 34)

For description, illustrations and synonymy see Hawksworth & Dyko (1979).

Teleomorph (perfect state): Abrothallus microspermus Tul. The anamorph of this species was illustrated and described by Tulasne (1852 : 116, pl. 16 figs. 22–26) in his original account of the fungus, giving the conidia as 6·5 × 3·5 μm. Hepp (*Flecht. Eur.* no.

*These reports were given under the name *Abrothallus smithii* Tul., a superfluous name for *A. bertianus* de Not. (which has smaller conidia; see p. 72) misapplied by these authors.

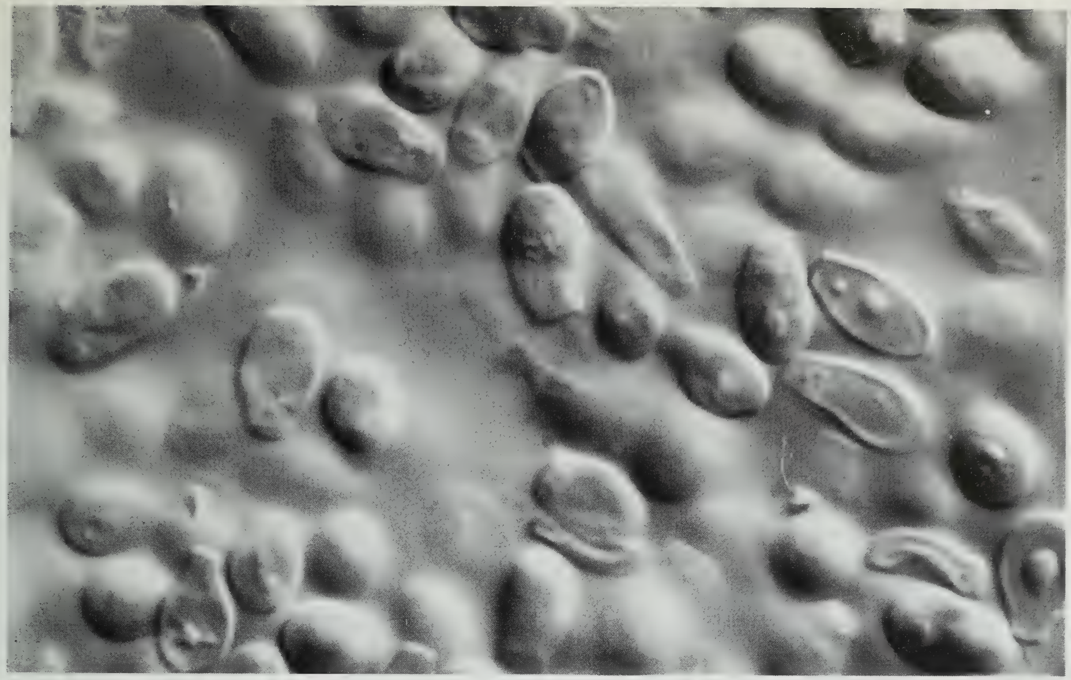

Fig. 34 *Vouauxiomyces truncatus* (Savoie, *Santesson,* UPS), conidia (× 2500).

471, 1857; K!) later distributed and illustrated material of both states. Pycnidia commonly occur without the teleomorph but are regularly encountered mixed amongst the ascomata. *Abrothallus microspermus* differs from *A. parmeliarum,* with which it has often been confused, in the consistently epruinose ascomata which only reach 300 μm diam; according to Keissler (1930) the ascospores are also paler brown and the epithecium K–.

Hosts: Parmelia caperata (L.) Ach., and more rarely *P. perlata* (Huds.) Ach., thalli. Little damage is usually encountered and the fungus is probably parasymbiotic.

Distribution: Austria, the British Isles (England, Ireland, Scotland, Wales), France, Germany and Switzerland. The report of the occurrence of this species in Sweden (Santesson, 1949 : 142) is based on material now referred to *Vouauxiomyces santessonii.*

Specimens (additional to those listed by Hawksworth & Dyko, 1979): **British Isles:** England, S. Devon, Slapton Ley Nature Reserve, The Causeway, on *Parmelia perlata* on *Salix,* 30 March 1972, *D. L. Hawksworth* 2696 *p.p.* (IMI 164972 *p.p.*!, UPS!); *loc. cit.,* Peasdish, on *P. caperata* on *Ulmus,* 23 August 1980, *D. L. Hawksworth* 5043 (IMI 251260!); Dorset, Wareham, on *P. caperata,* 1978, *V. Giavarini* (E!). Scotland, Dunbarton, Loch Lomond, Aber Island, on *P. perlata,* 10 October 1979, *B. J. Coppins* 4482 (E, IMI 243340!). Wales, Merioneth, Barmouth, nr Arthog, Fegla Fawr, on *P. caperata,* 12 December 1972, *B. J. Coppins* (E!).—**France:** Savoie, Dept. Haute-Savoie, N of Sciez, Chateau Coudrée, on *P. caperata* on *Tilia,* 9 June 1946, *R. Santesson* (UPS!).—**Switzerland:** *sine loc., P. Hepp* [*Flecht. Eur.* no. 471] (K!).

Additional reports of anamorphs

In addition to the anamorphs of *Abrothallus* and *Microcalicium* species treated in the preceding section, which can occur without their teleomorphs, there are literature reports of pycnidial anamorphs in a number of other lichenicolous ascomycetes. As many of these may be merely spermatial, the conidia not functioning as diaspores but rather as gametes, and consequently are normally to be found in association with

ascomata, it seems superfluous to provide them with independent binomials. No compilation of the lichenicolous ascomycetes in which such anamorphs have been reported appears to be available. As these states may cause confusion when studying lichenicolous Coelomycetes, or sometimes be found alone, reports of those I have been able to discover are listed here. The location of all such reports would be a major bibliographical exercise involving the study of the whole literature on lichenicolous fungi; the following should consequently not be viewed as an exhaustive list.

Abrothallus bertianus de Not. (syn. *A. glabratulae* Kotte, *A. smithii* Tul.)

Kotte (1909 : 81) gave the conidia in this species as 5·46–6·5 × 3·9–4·42 μm, but I have not found a pycnidial state in the few specimens of it I have seen. This fungus appears to be confined to brown species of *Parmelia* and is especially frequent on *P. glabratula* (Lamy) Nyl. (Santesson, 1960; Hawksworth & Minter, 1980).

Abrothallus cetrariae Kotte

In the original account of this species, described from *Platismatia glauca,* the conidia were given as 4·94–6·5 × 3·9–4·9 μm (Kotte, 1909 : 84). These measurements are too small for *Vouauxiomyces santessonii* (p. 69), which occurs on the same host.

Abrothallus peyritischii (B. Stein) Kotte

The pycnidia of this species, which occurs on *Cetraria nivalis* (L.) Ach., were illustrated by Kotte (1909 : pl. 1 figs. 12–17) and appear to belong to *Vouauxiomyces*; the conidia were said to measure 5·2–6·76 × 3·9–5·2 μm. One of Kotte's figures is reproduced by Keissler (1930 : 205 fig. 46).

Abrothallus usneae Rabenh.

This fungus, which has often been united with *A. parmeliarum,* was investigated anatomically by Galløe (1950 : 73, pls. 113–115). His drawings of vertical sections of pycnidia, conidiogenous cells and conidia leave no doubt that the pycnidia of this species belong to *Vouauxiomyces,* but no conidial dimensions were provided.

Arthonia clemens (Tul.) Th. Fr. (syn. *Conidia clemens* (Tul.) Massal., *Phacopsis clemens* Tul.)

In the original description of this species, based on material from species of *Lecanora* and *Rhizoplaca chrysoleuca,* Tulasne (1852 : 125) described the pycnidia as 70–80 μm tall, thick- and brown-walled, with straight, bacilliform conidia 3–4 μm long. They were also reported from this fungus in the hymenium of *Lecanora atra* (Huds.) Ach. by Werner & Deschatres (1974 : 317–8) who gave them as 4 × 0·5 μm.

Arthonia fuscopurpurea (Tul.) R. Sant. (syn. *Celidium fuscopurpureum* Tul.)

This species, which occurs on *Peltigera* thalli, is described as forming bacilliform conidia which are hyaline and to 3·5 μm long (Tulasne, 1852 : 121).

Arthonia varia (Tul.) Jatta (syn. *Phacopsis varia* Tul.)

Tulasne (1852 : 126, pl. 14 fig. 3) described straight bacilliform conidia about 4·5 μm long in this species on *Xanthoria parietina* (L.) Th. Fr. The relationship of this taxon to both *A. epiphyscia* Tul. and *A. destruens* Rehm, which also attack *Xanthoria* species, requires further study; contrary to Keissler's (1930 : 98) treatment, it is distinct from *A. glaucomaria* (Nyl.) Nyl. which is found on *Lecanora rupicola* (L.) Zahlbr.

'Celidium' insidens Vouaux

The pycnidia of this fungus were rather fully described by Vouaux (1914 : 170). They arose in groups of 5–6 and were lenticular-convex, immersed only at the base, 0·2–0·3 mm diam, black, and produced cuneiform hyaline 1-septate conidia 9–12 × 4·5 μm

from simple to 2-septate conidiogenous cells measuring 9–20 × 2–3 μm. The species was found on material of *Ramalina fraxinea* collected in Tenerife.

Dacampiosphaeria rivana (de Not.) D. Hawksw. (syn. *Homostegia lichenum* Fuckel)

According to Fuckel (1870 : 224) this fungus produces 1-septate, cylindrical, curved conidia which are 16 × 2·5 μm. In my investigations on this fungus I did not find any pycnidial state (Hawksworth, 1980*a* : 367–371), and it seems probable that Fuckel's report is based on an unidentified lichenicolous coelomycete on *Peltigera.*

Dichosporium glomerata Pat.

This species, which occurred on an undetermined corticolous lichen from Guadaloupe, is described as producing pycnidia on a superficial mycelium which give rise to hyaline, simple, subcylindrical conidia, measuring 5–6 × 2 μm (Vouaux, 1912 : 199).

Didymella parvispora Henssen

Henssen (1977 : 44, pl. 8K), in the original description of this fungus from *Zahlbrucknerella africana* Henssen, reported the pycnidia as partially immersed, elongate, 30–50 μm broad, with a dark brown ostiole, and elongate conidiogenous cells giving rise to bacilliform, hyaline conidia 1·5–2 × 0·5–1 μm.

Guignardia olivieri (Vouaux) Sacc.

Pycnidia resembling those of *Leptodothiorella,* scattered in thalline warts, immersed, ± globose, 75–100 μm diam; pycnidial wall subhyaline, pseudoparenchymatous, 8–12 μm thick; conidiogenous cells phialidic, short-ampulliform, 7–10 × 1·5–2·5 μm; conidia arising in short chains, bacilliform, hyaline, simple, often slightly compressed medianly, 3·5–5 × 1·5–2 μm. The anamorph of this species was described and illustrated by Hawksworth (1975*b*: 190–191, fig, 5G–J) on *Xanthoria parietina.* The conidiogenous cells were then described as holoblastic, but improved microscopic techniques indicate that they are almost certainly enteroblastic-phialidic.

Homostegia piggotii (Berk. & Broome) P. Karsten

This species was studied in some detail by Schaechtelin & Werner (1928) who noted pycnidia in developing stromata on *Parmelia saxatilis* (L.) Ach. These were pyriform, ostiolate, with slender conidiogenous cells radially orientated. Their illustration (*loc. cit.:* pl. 11 fig. 17) suggests that the conidiogenous cells may sometimes be multicellular and branched, but the hyaline, simple, subglobose conidia were reported to be formed apically. No measurements were provided.

Lethariicola sipei Grumm.

In the original account of this monotypic genus of odontotremoid fungi on *Letharia vulpina* (L.) Hue, Grummann (1969 : pl. XIV figs. 19–20) provided photographs of rather thick-walled erumpent pycnidia, but did not mention them in the written account of the species. The nature of the conidiogenous cells and the conidia cannot be deduced from the low-power photographs provided.

Lichenomyces lichenum (Sommerf. ex Fr.) R. Sant. (syn. *Celidium stictarum* Tul.)

Pycnidia have been noted in this species by several workers, notably Tulasne (1852 : 123, pl. 14 fig. 8), Werner (1928 : pl. IX figs. 2–4) and Vězda (1970 : 222, 225 fig. 4). The pycnidia are immersed to slightly erumpent at the ostiole in young stromata, and contain filiform, simple conidiogenous cells to 30 μm tall, which in turn produce bacilliform, hyaline, simple conidia 3–4 × 1 μm singly from their apices. This fungus is especially frequent on *Lobaria pulmonaria* (L.) Hoffm., and is known from a wide range of genera in the Stictaceae.

Merismatium lecanorae (H. Olivier) Vouaux

Vouaux (1913 : 78) discovered material of this fungus, on *Ochrolechia parella* (L.) Massal., with pycnidia which were black, 250–350 μm diam, and formed ovoid conidia which were hyaline and simple at first, but later became brown and 3-septate to muriform when mature, and 11–15 × 6–7 μm. He was not, however, convinced of the relationship between the pycnidia and the putative teleomorph.

Muellerella lichenicola (Sommerf. ex Fr.) D. Hawksw. (syn. *Tichothecium erraticum* Massal.)

Vouaux (1913 : 63) found pycnidia in a collection of *Caloplaca vitellinula* auct. associated with the species now called *Muellerella lichenicola.* These gave rise to brown, 1-septate, ellipsoid conidia measuring 6–7 × 2·5–3 μm. Vouaux had little doubt that he was dealing with an anamorph of *M. lichenicola,* but the details he provides show that his material belonged to *Lichenodiplis lecanorae* (see p. 38).

Nesolechia oxyspora (Tul.) Massal.

Kotte (1909 : 93, pl. 3 figs. 29–30) noted pycnidia in the thecium of this species, which normally occurs on thalli of *Parmelia saxatilis.* These produced rather irregularly shaped broadly ellipsoid to subglobose hyaline conidia, but no further details were provided. He may have been dealing with an unknown fungicolous coelomycete on the *Nesolechia,* rather than an anamorph of *N. oxyspora.*

Scutula epiblastematica (Wallr.) Rehm (syn. *S. wallrothii* Tul.)

According to Tulasne (1852 : 119–120, pl. 14 figs. 18–24) and Vouaux (1913 : 424), this fungus, which occurs on *Peltigera* thalli, has two types of pycnidia. One, which they considered to be spermagonial, had pycnidia 60–90 μm diam with hyphal walls and formed cylindrical, slightly curved, simple, hyaline conidia, 8–12 × 0·5–1 μm; the second type of pycnidium was larger, 100–150 μm diam, with the walls composed of thick-walled pseudoparenchymatous cells, and gave rise to narrowly ellipsoid, often slightly curved, simple or rarely 1-septate, hyaline conidia, 12–16 × 2·5–4 μm, from conidiophores measuring 6–10 × 2 μm. There is a strong resemblance between the reported macroconidial phase and the description of *Diplodina peltigerae* (see p. 76). The pycnidial wall structure for this assumed state, as illustrated by Tulasne (*loc. cit.*), recalls that of *Karsteniomyces peltigerae* (see p. 22) and it is conceivable that he had a mixed collection in which the conidia of the *Karsteniomyces* had not attained their normal length and most not their final septum.

Stigmidium dispersum (Lahm ex Körber) D. Hawksw. (syn. *Pharcidia dispersa* (Lahm ex Körber) Winter)

Pycnidia were apparently first reported for this species by Vězda (1963 : 151–153, fig. 4), who described them as semi-immersed, 80–120 μm diam, and forming bacilliform, simple or 1-septate, hyaline conidia, 10–15 × 1·5 μm.

'Telimena' foreaui F. Moreau

In the original account of this species, described from specimens of *Heterodermia speciosa* (Wulfen) Trevisan collected in India, Moreau (1951 : 209) reported that pycnidia were present in the stroma. These were *c.* 50 μm diam, immersed, and formed bacilliform, hyaline conidia, 4 × 1 μm.

Excluded species

All taxa referred to coelomycete genera which have been considered as lichenicolous by their original or later authors, and which have not been treated in the preceding

sections of this contribution, are compiled here alphabetically; obligate synonyms are listed by their basionyms and not separately.

Aposphaeria ramalinae Vouaux, *in* Pitard & Harmand, *Bull. Soc. bot. Fr., Mém.* **22** : 72 (1912) ['1911'].

Type: Canary Islands, Tenerife, Vueltas de Taganana, 'sur le *Ramalina implectens*, dans la zone sylvestre', alt. 700 m, 1907, *J. Pitard.*

This fungus was originally described as forming a brownish superficial reticulum of hyphae 1·5–3 μm wide, and from which elongate fusiform brownish 1(–3) septate conidia 9–12 × 2–3·5 μm were formed in short chains. In the centre of the mycelium pycnidia 80–130 μm were produced which contained hyaline, simple, broadly ovate conidia, measuring 3–3·5 × 2·5 μm. No material of this taxon could be located amongst Harmand's herbarium in Angers (M. Guerlesquin, *in litt.*), but according to the original description the name seems to have been based on two different fungi: an unidentifiable dematiaceous hyphomycete and a coelomycete. The conidia of the latter recall those of *Vouauxiomyces ramalinae* (see p. 67), but the pycnidia were larger than usual for that species.

Chaetothyriolum puiggarii Speg., *Boln Acad. nac. Cienc. Cordoba* **23** : 522 (1919).

This monotypic genus was considered by Petrak & Sydow (1935 : 192) to be based on the pycnidia of a lichen. The type material was re-examined by Santesson (1952 : 53) and found to be too fragmentary for reliable determination.

Chlorocyphella aeruginascens var. **cystidiifera** Keissler, *Annln naturh. Mus. Wien* **41** : 162 (1952).

This fungus, described from material of *Lopadium phyllogenum* (Müll. Arg.) Zahlbr. collected in the Solomon Islands, is almost certainly a species of *Pyrenotrichum.* According to Keissler (*loc. cit.*), it differs from the species now known as *P. splitgerberi* in having sterile cystidia-like structures between the conidiogenous cells, and much longer conidia, 120–140 × 1·5 μm. I have not examined the type material and the name was not discussed by Santesson (1952 : 41, 49–53).

Coniothyrium epiphyllum Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 296 (1914).

This name is of uncertain application, no fungus recalling the original description being present on the holotype (Hawksworth, 1977 : 193).

Coniothyrium harmandii Zopf ex Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 295 (1914).

This name is of uncertain application in the absence of type material (Hawksworth 1977 : 193–194).

Coniscosolen mirabilis Schilling, *Hedwigia* **67** : 297 (1927).

This monotypic genus was based on the normal pycnidia of an unidentified *Psorotheciopsis* Rehm species according to Santesson (1952 : 331) who examined the type material.

Cristidium pallidum R. Sant., *Symb. bot. upsal.* **12**(1) : 357 (1952); nom. inval. (Art. 32).

This name was mentioned as an undescribed genus and species of imperfect fungi on *Gyalectidium filicinum* Müll. Arg., but no further details were given and it is thus uncertain if this was a coelomycete or hyphomycete. It is conceivable that this might be *Hansfordiellopsis lichenicola* (Bat. & Maia) Deighton, which is well known on *Gyalectidium* (Hawksworth, 1979 : 224–227).

Dendrophoma lecanorae Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 284 (1914).

This species was described on the basis of two different French collections, neither present among the remnants of Vouaux's herbarium (Rondon, 1970); on *Lecanora piniperda* Körber (syn. *L. glaucella* (Flotow) Nyl.) from Meyrueis, Lozère, and on

Lecania fuscella (Schaerer) Körber (syn. *L. syringea* (Ach.) Th. Fr.) from Malo-Terminus. The erumpent pycnidia were described as 100–172 μm, with a hyphal wall, 2–3-irregularly branched conidiophores 12–25 × 2 μm, and ovoid hyaline simple conidia 3–5 × 1·5–2 μm. In the absence of material this name remains of uncertain application; the conidiophore description and conidium shape indicates that *Lecania* conidia were probably not involved (Eigler, 1969 : pl. 5).

Diplodia parmeliae Berk. & M. A. Curtis, *in* Berkeley, *Grevillea* **3** : 3 (1874).
Type: U.S.A., South Carolina, on *Parmelia* cf. *rudecta* Ach., *M. A. Curtis* (K—holotype!).
Diplodina parmeliae (Berk. & M. A. Curtis) Sacc., *Syll. Fung.* **3** : 413 (1884).

This species was introduced with an extremely brief description which included no information on the sizes of spores or other features. The perithecia were reported to have depressed ostioles and to be loosely clothed with flexuous threads, but their colour was not indicated, and the spores stated to be hyaline with 1 septum and unequal cells. Examination of the holotype established that the perithecia were translucent-orange, about 200 μm wide, with whitish lax hairs, and that ascospores in two size ranges were formed, macroascospores about 51 × 23 μm and microascospores 9–11 × 4–6 μm. The fungus agrees in all details with *Nectria heterospora* Speg., a species described and discussed by Hawksworth & Booth (1976), but as the epithet *heterospora* dates from 1889, the new combination **Nectria parmeliae** (Berk. & M. A. Curtis) D. Hawksw. **comb. nov.** must be adopted for this species.

Diplodina peltigerae Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 289 (1914).
Type: France, Vosges, Plainfaing, on *Peltigera canina* (L.) Willd., *J. Harmand & L. Vouaux.*

This species is not represented in the remnants of Vouaux's herbarium (Rondon, 1970) and it could not be located amongst Harmand's collections in Angers (M. Guerlesquin, *in litt.*). It was described as forming black, immersed pycnidia 60–100 μm diam, which produced hyaline, ellipsoid conidia with a single septum often located below the centre and 10–14 × 3–4 μm. If it is re-collected it should be possible to recognize it from these details and then re-assess its position. No similar fungus is known to occur on *Peltigera* (Hawksworth, 1980*a*); the measurements are suggestive of the reported macroconidial anamorph of *Scutula epiblastematica* (p. 74).

Epicoccum parmeliarum H. Olivier, *Bull. internat. géogr. Bot.* **17** : 232 (1907).
Type: France, Orne, on *Parmelia caperata* and *P. sulcata* (thalli), *H. Olivier.*
Phoma parmeliarum (H. Olivier) Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 196 (1914).

Vouaux (*loc. cit.*) considered that this name was based on the anamorph of *Abrothallus parmeliarum.* There can be little doubt Olivier was dealing with a *Vouauxiomyces* species since the conidia were originally described by him as 'terminées en pédoncule à la base'; the pycnidial size quoted (0·2–0·4 mm diam) and the lengths and breadths of the conidia (6–9 × 5–7 μm) certainly recall the measurements for *V. santessonii* (teleomorph *A. parmeliarum*), but the mention of *Parmelia caperata* suggests that he may really have been dealing with either *V. truncatus* (teleomorph *A. microspermus*), or a mixture of both these anamorphs on different hosts. As Olivier's epithet would pre-date both '*santessonii*' and '*truncatus*' at species level it seems unwise to take it up here in either sense in the absence of Olivier's material.

Libertiella obscurior Gerber, *Arch. Protistenk.* **74** : 485 (1931).
Type: Austria, Hohen Tauren [Hohentauren], Naturschutzpark, on *Hypogymnia intestiniformis* (Vill.) Räsänen (syn. *H. encausta* (Sm.) W. Watson), 1929, *F. Mattick.*

The holotype was formerly preserved in the herbarium at DR but the lichen material there was destroyed in 1945 and no duplicate appears to have existed (F.

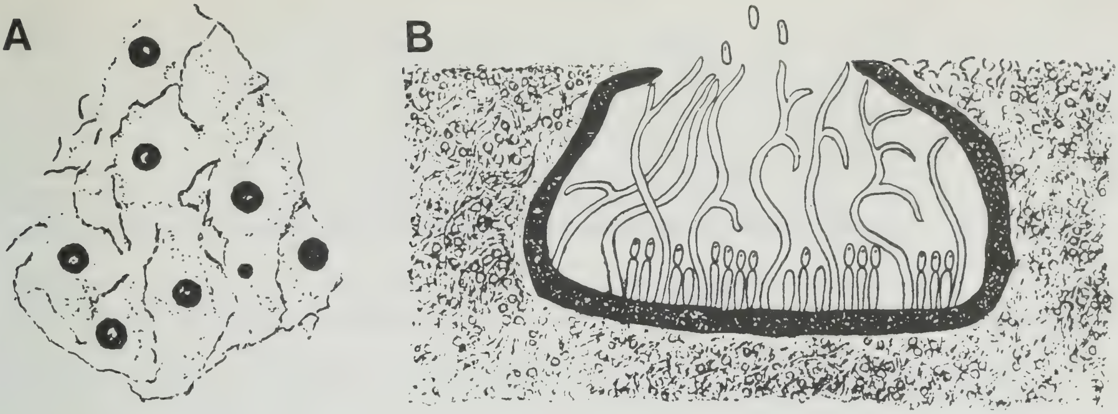

Fig. 35 *Lichenophoma haematommatis.* **A,** Pycnidia on the host. **B,** Vertical section of pycnidium. Scale not indicated. Reproduced from Keissler (1911 : 297).

Mattick, *in litt.*). This taxon was described as producing numerous immersed pycnidia, 0·15–0·2 mm diam, pale at the base but brownish above, delicate and hyphal, and producing ellipsoid, hyaline conidia measuring 2·5–3·4 × 1·7–2 μm. No conidiophores were recognized. Pycnidia are often numerous in *Hypogymnia intestiniformis* but the conidia measure 5–6·5 × 0·8–1 μm (Hillmann, 1936 : 80). If Gerber's figures are reliable, there can consequently be little doubt that his assertion was correct in that he was not dealing with the normal pycnidia of the host. The name must, however, remain of uncertain application until fresh material that might be referrable to Gerber's taxon is discovered, and the method of conidiogenesis determined.

Libertiella xanthoriae Keissler, *Annln naturh. Mus. Wien* **38 :** 166 (1925).

Type: Sweden, Vestmanland, Vesteras, on *Xanthoria fallax* (Hepp) Arnold [?], 2 August 1924, *J. A. Nannfeldt* (W 1925/10417—holotype!).

The *Xanthoria* thalli appear to be quite healthy and are their normal colour, except for some deeper orange convex swellings (200–600 μm wide). In vertical section these were seen to comprise a very irregular compact conidiiferous structure and to produce numerous hyaline subcylindrical to rather ellipsoid conidia 3–4 × 1–2 μm which arose laterally on integrated doliiform conidiogenous cells. This area was not sharply delimited from the host tissues internally and the hyphae merged indistinguishably with the rest of the thallus, which included healthy algal cells in the immediate vicinity of the pycnidia.

Pycnidia (spermogonia) are not common in *X. fallax* but were figured by Galløe (1948 : pl. 98 fig. 641) as deeper orange convex swellings superficially identical to those on Nannfeldt's specimen. As the conidiogenous cells are similar to those of other *Xanthoria* species (see e.g. Galløe, *op. cit.)* it is evident that Keissler's name was based on the normal pycnidia of the host; the species of *Xanthoria* may not have been *X. fallax,* however, as the conidia in that species are reported to be a rather more elongate (Moberg, 1977 : 13).

Lichenophoma haematommatis Keissler, *Hedwigia* **50 :** 296 (1911).
(Fig. 35 A–B)

Type: Austria, 'in valle flumius "Enns", dicto "Gesäuse", ad Gesäuse-Eingang', on *Haematomma elatinum* (Ach.) Massal. thallus, July 1910, *K. Keissler.*

The new genus *Lichenophoma* Keissler was introduced by Keissler (*loc. cit.*) for this single species. Unfortunately the type material could not be located in W (U. Passauer, *in litt.*) and, as noted by Sutton (1977 : 113–114), the structure of the wall, conidiogenesis, and relationship of the sterile paraphyses-like filaments figured (Fig.

35B) to the conidiophores all require clarification before any firm opinion on the genus can be reached. The pycnidia were described as immersed, *c.* 120–150 × 60–80 μm, with conidiogenous cells 12–15 × 1 μm (!) forming oblong conidia which were hyaline and *c.* 5 × 2 μm; the sterile filaments, *c.* 60–70 × 1 μm, branched and approached the ostiole. I have not seen any fungus on *Haematomma elatinum* that could be identical with Keissler's taxon. There is a second report of this species by Keissler (1933 : 390) from a sterile lichen thallus on *Quercus* in France (Oise, Forêt de Compiègne, au mont St Marc, November 1923, *E. Cottereau*) but that collection also has not been located.

Lichenophoma opegraphae Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 285 (1914).

This taxon was based on two collections of Bouly de Lesdain from northern France: on *Opegrapha* sp. at Merckeghem, and on *O. niveoatra* (Borrer) Laundon (syn. *O. subsiderella* (Nyl.) Arnold) from Ghyvelde. The pycnidia were described as immersed, 100–150 μm diam, with pseudoparenchymatous brownish walls composed of polyhedral cells 3–6 μm thick. Oblong conidia somewhat narrowed at the base, often unequal-sided, simple, hyaline, and 3·5–5 × 1·5–2 μm, were given as produced from simple conidiophores, 10–22 × 1·5 μm. Sterile branched and anastomosing hyphae 2–2·5 μm thick formed 'un réseau irrégulier'. This taxon is not represented in the remnants of Vouaux's herbarium (Rondon, 1970) and as that of Bouly de Lesdain was destroyed in 1940 the application of this name must remain uncertain. It is, however, probable that Vouaux was dealing with the microconidial state of the host which forms unequal-sided conidia mainly 4–6(–7) × 1–1·5 μm. It is most unlikely that he had the fungus treated here as *Laeviomyces opegraphae* (p. 28) as that has much shorter conidiogenous cells, pale brown conidia with equal sides and a distinctly truncated base, and no network of hyphae in the pycnidial cavity.

Microthelia solorinaria Lindsay, *Q. Jl microsc. Sci.* II, **9** : 350 (1869).

Type: Ireland, Co. Kerry, Brandon Mountain, on *Solorina crocea* (L.) Ach., *I. Carroll* (E—holotype!).

Diplodina solorinaria (Lindsay) Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 289 (1914).

In the original place of publication of this name, Lindsay (*loc. cit.*) stated merely '*M. solorinaria,* Linds., Spermog., 175. On thallus of *Solorina crocea.* Pycnidia only.' Although no description was provided here, as the earlier publication of Lindsay (1859 : 175) is cited, and a description was given there, the name must be accepted as validly published. Lindsay (1859 : 175) cited two specimens 'Brandon Mountain, Kerry, Ireland, CARROLL; Wicklow, D. MOORE, in Herb. Carroll' but only one of these (unspecified) had the fungus concerned. Both were thought to be lost (Hawksworth, 1980*b* : 174) but the former was recently re-discovered misfiled under *Pleospora hookeri* (Borrer) Keissler in E; as this has a fungus conforming to Lindsay's description and drawings it must be the holotype. This collection supports what is certainly *Rhagadostoma lichenicola* (de Not.) Keissler; although no intact asci were seen the ascospores were typical for that species and 'Munk-pores' were present on the peridial cells. *Dacampiosphaeria rivana* (de Not.) D. Hawksw. is also present on the specimen but does not predominate nor conform to Lindsay's account. The name *M. solorinaria* is consequently correctly interpreted as a later synonym of *R. lichenicola.*

Phaeoantenariella lichenicola Cavalcante, *Publções Inst. Micol. Recife* **633** : 3 (1969).

Type: Brazil, Maranhão, alto Turí, on *Mazosia melanophthalma* (Müll. Arg.) R. Sant. on indet. leaves, 27 December 1967, *J. de Anchieta* (URM 80709 n.v.).

The monotypic new genus *Phaeoantenariella* Cavalcante was introduced for a fungus with broad, torulose, dark brown hyphae spreading over the surface of the host, and which was reported to produce minute intercalary pycnidia, only 1–3 times the width of the hyphae, and conidia which were brown, simple, and 2–4 × 1·5–2 μm. A

specimen received from Recife and labelled 'tipo' from the type locality was examined but this bore the date 8 April 1967 and was numbered URM 71963 (exs. 41664!), contrary to the type description. This material had, however, been studied by Cavalcante in July 1968, prior to the publication of the name, and supported hyphae certainly identical to those figured by Cavalcante (*loc. cit.*: 4–5). The 'pycnidia' described appeared to be only compact dividing regions of cells, and the 'conidia' must be assumed to be merely cells that had become dissociated by pressure during slide preparation.

This name is consequently rejected as based on sterile mycelium.

Phoma abietinae Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 282 (1914).

Type: Switzerland, 'ad truncos abietinos in m. Gurnigel', *L. E. Schaerer* [*Lich. Exs.* no. 534] (E—holotype!).

Exsiccata: Schaerer, *Lich. Exs.* no. 534 (E!; sub *Lecidea leucocephala C. patelliformis*).

Vouaux (1914 : 282) based his account of *Phoma abietinae* on Lindsay's (1872 : 259) description of pycnidia in the above exsiccatum; he did not indicate that he had studied any examples for himself of this number. Pycnidia are now rather sparse in the holotype, scattered over the thallus of *Lecanactis abietina* (Ach.) Körber, which has numerous apothecia, and agree in all details with the pycnidial state of this lichen (see Coppins & James, 1979); the C+ red reaction obtained from the pruina covering the aging pycnidia, the shape of the pycnidia, and size of the conidia, all show that this is not *L. subabietina* Coppins & P. James, a species with C− pycnidial pruina not known to form apothecia. The name *Phoma abietinae* should consequently be added to the synonymy of *Lecanactis abietina,* and excluded from the lichenicolous fungi.

Phoma alectoriae Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 197 (1914).

Type: Switzerland, 'ad Abietum truncos in m. Gurnigel', on *Bryoria capillaris* (Ach.) Brodo & D. Hawksw., *L. E. Schaerer* [*Lich. Exs.* no. 496] (E—lectotype!).

Exsiccata: Schaerer, *Lich. Exs.* no. 496 (E!; sub *Parmelia jubata δ. cana*).

Icones: Lindsay, *Trans. R. Soc. Edinb.* **22** : pl. IV figs. 17–18 (1859).

Vouaux's (1914 : 197) tentative introduction of this name for a species he considered allied to *Phoma usneae* (see p. 57) was based entirely on Lindsay's (1859 : 134) description and illustrations. The flattened blackened warts mentioned by Lindsay now occur rather sparsely on the lectotype and in none could any pycnidia or conidia be found. These warts do, however, closely resemble the young ascocarps of *Phacopsis huuskonenii* Räsänan, which is well-known on the same host (Hawksworth, 1978*a*). The 'sterigmata' figured recall the paraphyses of *P. huuskonenii,* and furthermore the spore size given (15–23 × 3 μm) is reminiscent of that of this same species ((12–)14–16(–18) × 2–3·5 μm, *fide* Hawksworth, *loc. cit.*), although the conidia in Lindsay's figure do not belong here. Lindsay's figure was, however, also based on Schaerer's *Lich. Exs.* no. 392 (sub *Parmelia mollis γ. divaricata;* E!), but this packet no longer contains any intermixed *Bryoria.*

This name, which in any case might be interpreted as not validly published under Art. 34, is considered to have been based on *Phacopsis huuskonenii* and some other fungus. As neither of these elements constitutes a satisfactory type, Vouaux's name must be rejected.

Phoma arachnoidea Gerber, *Arch. Protistenk.* **74** : 483 (1931).

Type: Austria, Sölden, on *Hypogymnia intestiniformis* (Vill.) Räsänen (syn. *H. encausta* (Sm.) W. Watson), *W. Zopf.*

No material under this name could be located in B (B. Hein, *in litt.*) or DR (see p. 88). The pycnidia were described as about half-immersed and producing ellipsoid, hyaline, and often pointed conidia 3·5–4·25 × 1·75–2·5 μm, formed apically on filiform, non-septate, smooth conidiophores, measuring 12 × 2·5 μm. If Gerber's measurements are

correct and his description of the conidiophores accurate, he must have been dealing with a lichenicolous fungus and not the normal pycnidia of the host (see p. 77). Gerber's name consequently remains of uncertain application, but the long conidiophores certainly exclude it from *Phoma*.

Phoma biformis Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 282 (1914).

Type: France, Moëres, on *Anisomeridium biforme* (Borrer) R. C. Harris thallus on *Salix alba* wood, *M. Bouly de Lesdain*.

No material of this taxon is present amongst the remnants of Vouaux's herbarium (Rondon, 1970), and that of Bouly de Lesdain was destroyed in 1940. The pycnidia were described as 50–140 μm wide, and as producing ovoid to globose conidia 1–1·75 × 1–1·5 μm on conidiogenous cells 5–12 μm long. Normal pycnidia of this lichen are not uncommon but may be of two types: microconidia which are orbicular and 2–3 μm, or macroconidia which are orbicular to elliptical or ovate and 3–5 μm diam or 3·5–5 × 2·5–3 μm (Harris, 1975 : 104). Vouaux's measurements suggest that he was not therefore dealing with the pycnidia of the reported host, but it is quite possible mistakes were made in measuring such small conidia. The name remains of uncertain application.

Phoma caperatae Vouaux, *in* Bouly de Lesdain, *Bull. Soc. bot. Fr.* **59** : 16 (1912).

Type: France, Versailles, Fausses-Réposes wood, on *Parmelia caperata* (L.) Ach. on oak, *M. Bouly de Lesdain*.

Phoma physciicola var. *caperatae* (Vouaux) Keissler, *Beih. Bot. Zbl.* II. **37** : 273 (1920).

This species is not represented in the remnants of Vouaux's herbarium (Rondon, 1970), and that of Bouly de Lesdain was destroyed in 1940. The description of the pycnidia as superfical, black, subglobose and 0·1–0·25 mm diam is suggestive of *Vouauxiomyces truncatus* (see p. 70), but the ovoid conidia were described as 'basi saepe angustatis atque acutiusculis'—most inappropriate for that species. The conidia were given as 3–6 × 2·5–3 μm, and the conidiogenous cells as 3–4 × 2 μm. Bouly de Lesdain (*loc. cit.*) mentions a second collection on the sterile thallus of a *Calicium* species on oak at Rodez, Aveyron; these dimensions are suggestive of the normal conidia of *Calicium* rather than any lichenicolous fungus known from this host. The collection on *Parmelia* at least must have been a lichenicolous fungus, but its position remains uncertain in the absence of the original material.

Phoma curvispora Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 281 (1914).

In the original description of this species Vouaux cited three specimens, all collected by Bouly de Lesdain: on *Lecanora saligna* (Schrader) Zahlbr. from Versailles, on *Lecania* sp. from Zuydcoote, and on *Lecidella elaeochroma* (Ach.) M. Choisy from Ghyvelde. Unfortunately Bouly de Lesdain's herbarium was destroyed in 1940, and this taxon is not represented amongst the remnants of Vouaux's herbarium (Rondon, 1970). Keissler (1930 : 547) states that he saw the 'Originalexamplar' himself, and that it represents only pycnidia of the lichen in question but does not indicate which of the three original specimens he was able to see. The description of the conidia as 'très courbes, souvent en demi-cercle', and 8–15 × 2–3 μm, leaves little doubt that the name *Phoma curvispora* was partly based on the pycnidia of *Lecanora saligna*.

Phoma epiparmelia Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 282 (1914).

Type: Yugoslavia, Nadin, Gradina, on *Peltigera pusilla* Körber, *Baumgartner*.

This fungus was described as not damaging the host thallus and comprising erumpent, black, globose pycnidia 60–130 μm diam, with pseudoparenchymatous walls made up of brown cells 7–10 × 4–6 μm. Unbranched conidiophores, simple or rarely 1-septate, sinuous, and 6–10 × 1·5–2 μm gave rise to rather irregularly shaped ellipsoid to frequently unequal-

sided simple hyaline conidia measuring 3·5–4·5 × 2–3 μm. Unfortunately the original material could not be located in W (H. Riedl, *in litt.*), and is not present amongst the remnants of Vouaux's herbarium (Rondon, 1970). The long conidiogenous cells, smaller pycnidia, and lack of damage to the host, separate this taxon from *Phoma peltigerae* (see p. 54). In the absence of the original material the name must be treated as of uncertain application until a fungus conforming to Vouaux's description is re-discovered.

Phoma epiphyscia Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 197 (1914).

Type: France, Ghyvelde, on *Phaeophyscia orbicularis* (Necker) Moberg and *Xanthoria parietina* (L.) Th. Fr., *M. Bouly de Lesdain.*

This taxon is not represented amongst the remnants of Vouaux's herbarium (Rondon, 1970), and as that of Bouly de Lesdain was destroyed in 1940, the type material is presumed to be lost. The species was described as having immersed black pycnidia 80–150 μm, with pseudoparenchymatous walls, and conidia hyaline, simple, 2-guttulate, 4–6 × 2–3 μm, formed from short conidiogenous cells. The conidial dimensions given are too large for *Phaeophyscia orbicularis* and *Xanthoria parietina.* Vouaux (*loc. cit.*) suggested that it might represent an anamorph of the species now called *Arthonia epiphyscia* Nyl.; I have not seen pycnidia associated with *A. epiphyscia*, but they may occur (see p. 72). A further possibility is that Vouaux was dealing with the anamorph of *Guignardia olivieri* (see p. 73), as suggested by Hawksworth (1975*b* : 191).

Phoma fusispora Vouaux, *in* Bouly de Lesdain, *Bull. Soc. bot. Fr.* **59** : 215 (1912); nom. illegit. (Art. 64).

Non *Phoma fusispora* Rostrup, *Bot. Faeröes* **1** : 313 (1901).

This species was originally described from specimens of *Lecanora saligna* (Schrader) Zahlbr. and *L. dispersa* (Pers. ex Sommerf.) Nyl. collected by Bouly de Lesdain 'aux environs de Dunkerque'. It was also mentioned by Bouly de Lesdain (*loc. cit.*) as on *Buellia punctata* (Hoffm.) Massal. Vouaux (1914 : 196) added *Bacidia spododes* (Nyl.) Zahlbr.* as a host and Bouly de Lesdain (1914 : 165) *Opegrapha niveoatra* (Borrer) Laundon. Bouly de Lesdain's herbarium was destroyed in 1940, and this species is not represented in the remnants of Vouaux's herbarium (Rondon, 1970). However, Keissler (1930 : 547) reports that he was sent the 'Originalexemplar' by Bouly de Lesdain and that the name was based on the pycnidia of the host, but does not indicate which host he received. The conidia were originally described as 'fusiformibus, paulum arcuatis, continuis, hyalinis' and 7–8 × 2 μm, characters seen in numerous lichen pycnidia. In the absence of material some doubt must remain, but the evidence suggests that this name was based on the pycnidia of several different lichens.

Phoma glaucella Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 198 (1914).

Three French collections were mentioned in the original account of this species: on *Bacidia inundata* (Fr.) Körber at Malo-Terminus, on *Lecanora* sp. at Ghyvelde, and on *L. piniperda* Körber (syn. *L. glaucella* (Flotow) Nyl.) at Meyrueis, Lozère; the first two collections were made by Bouly de Lesdain and the last by Marc. The species was described as having mainly immersed, black pycnidia 60–140 μm diam, simple or rarely bifurcate conidiogenous cells 5–10 × 1·5–2 μm, and ellipsoid, hyaline conidia 1·5–3 × 1–1·5 μm. As no material is present in the remnants of Vouaux's herbarium (Rondon, 1970), and that of Bouly de Lesdain was destroyed in 1940, the application of this name remains uncertain.

Phoma lecanorae Vouaux, *in* Bouly de Lesdain, *Rech. Lich. Dunk.*: 277 (1910).

Type: France, Dunkerque, dunes près le Phare, 'sur *Lecanora umbrina* var.', 18 June 1904, *M. Bouly de Lesdain* (herb. Vouaux—syntype!).

* = *Micarea nitschkeana* (Lahm ex Rabenh.) Harm.

Two specimens were mentioned in the original description of this taxon, the above and one from Malo-Terminus reported as on *Rinodina exigua* (Ach.) Gray; this latter collection is not represented in Vouaux's herbarium (Rondon, 1970), and as Bouly de Lesdain's herbarium was also destroyed, must be presumed lost. The collection from near Le Phare comprises a blackish-brown thallus on flint over which the pycnidia are evenly scattered; fruits of *Lecanora polytropa* are scattered amongst the dark thallus and were presumably mistaken for *L. dispersa* (Pers.) Sommerf. (syn. *L. umbrina* Nyl.) by Vouaux, but appear to be quite unrelated to the pycnidia. The evenly distributed pycnidia and healthy thallus leave no doubt that this material is the pycnidial state of a lichenized species; the thallus colour and short conidia (3–4 × 1–1·5 μm) are suggestive of *Opegrapha lithyrga* Ach.

Bouly de Lesdain (1914) and Vouaux (1914) reported eleven further hosts from a wide range of genera (interestingly, these included two *Opegrapha* species); these cannot be said to have comprised only lichen pycnidia in the absence of the collections cited.

Phoma lichenis Pass., *Atti Accad. naz. Lincei Rc.* **7 :** 48 (1891).

Type: Italy, prov. Parma, Vigheffio, Frassino, 'sul tallo di un Lichene sterile, fosse *Parmelia pulverulenta' [Physconia pulverulacea* Moberg], *G. Passerini.*

The type material could not be located in either PAD (S. Chiesa, *in litt.*) or PARMA (F. Lona, *in litt.*). The black pycnidia were described as having membranaceous pseudoparenchymatous walls and producing narrow bacilliform conidia 5 μm long. Conidia 4–7 × 1·5 μm are, however, characteristic of the pycnidia in both *Physcia* (Schreber) Michaux and *Physconia* Poelt (Moberg, 1977), and it therefore seems probable that this name was merely based on the pycnidia of the host. If this is so, as Art. 59 does not apply to lichen-forming fungi, Passerini's name may provide an earlier epithet for *Physconia pulverulacea.*

There are reports of this taxon from a wide range of hosts, some of which may refer to true lichenicolous fungi. Keissler (1930 : 541–2) mentions also *Cladonia rangiferina* (L.) Wigg., *Lecanora pallida* (Schreber) Rabenh., *Physcia stellaris* (L.) Nyl., and *Xanthoria parietina* (L.) Th. Fr.; Keissler (1933 : 386) adds *Cladonia rangiformis* Hoffm. and *Parmelia laevior* Nyl.

Phoma lichenis f. **immersa** B. de Lesd., *Rech. Lich. Dunk. :* 277 (1910).

Type: France, Dunkirk, on *Hypogymnia physodes* (L.) Nyl., *M. Bouly de Lesdain.*

As Bouly de Lesdain's herbarium was destroyed in 1940, the type collection is presumably lost. The only description provided was 'Les périthèces sont enfoncés au lieu d'être superficial'. Assuming that the conidia were roughly the same size as those given for *Phoma lichenis,* there can be little doubt that this form was based on normal pycnidia of the host.

Phoma verrucariae Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30 :** 281 (1914).

Type: France, Bergues, on *Verrucaria* sp. [?], *M. Bouly de Lesdain.*

This species was described as producing 2–3 pycnidia per areole of the sterile host, the pycnidia as immersed to almost superfical, black, 60–110 μm diam, with conidiophores 10–20 μm long, and conidia which were cylindrical, attenuated at the ends, slightly or strongly curved, hyaline, simple, and 12–14 × 1·8–2·5 μm. The host may not have been a *Verrucaria* as it was sterile and so could not have been checked microscopically; the name could therefore have been based on pycnidia of the 'host' and not a lichenicolous fungus. As this taxon is not represented in the remnants of Vouaux's herbarium (Rondon, 1970), and that of Bouly de Lesdain was destroyed in 1940, the application of this name remains uncertain.

Phoma versoniana Sacc., *Michelia* **2** : 342 (1881); nom. inval. (Art. 32).

Keissler (1930 : 582) lists the name as a possible synonym of the species now called *Libertiella malmedyensis*, but it does not appear to have been ever validly published and the only mention of it I have been able to locate is the reference cited above where the phrase '*Phomae Versonianae* meae analogo videtur' appears. It is not even known whether *P. versoniana* was considered to be lichenicolous.

Phyllosticta galligena F. Moreau, *Bull. Soc. bot. Fr.* **98** : 102 (1951).

Type: India, Palni Hills, Shembaganur, on *Parmelia perforata* Taylor, 1933, *G. Foreau.*

Icones: Moreau, *Bull. Soc. bot. Fr.* **98** : 101 (1951).

The type material of this gall-forming species could not be located in PC (J. Mouchacca, *in litt.*), nor was it available from Dr C. Moreau. Convex galls 0·25–1·5 mm were formed each including several black pycnidia (to 150 μm diam) forming simple, ellipsoid, hyaline conidia 1·5–3·5 × 1–2 μm. The conidiophores were described as unbranched and filiform, so it is clear that this species cannot be referred to *Phoma* (see p. 49). In the absence of further information it is impossible to suggest an appropriate genus for this species, but it should be possible to recognize it if re-collected and then re-assess its position.

Phyllosticta lichenicola Allescher, *Ber. bayer. bot. Ges.* **4** : 32 (1896).

Type: Germany, München, Ebenhausen, on *Parmelia perlata* (Huds.) Ach., 11 April 1895, *J. N. Schnabl* (M—holotype!).

This fungus was originally described as forming in necrotic patches about 2 mm diam, and having globose, black pycnidia with conidia hyaline, oblong, biguttulate, and 2–4 × 0·5–1·5 μm. Keissler (1930 : 535) studied the type material superficially but made no microscopic preparation because it was so small; no later authors appear to have found any fungus matching Allescher's description exactly, so a careful study of this specimen was needed. Only a single infection spot 2 mm diam remained on the thallus, this was necrotic with a black margin about 125–200 μm wide and contained six small black immersed sporocarps. Three of these proved to be ascomata of a *Polycoccum* or *Endococcus* species (paraphyses doubtfully present and not clearly demonstrable) with asci about 30 × 7 μm and 1-septate, pale brown, echinulate ascospores about 8 × 3 μm; the asci were 6–8 spored. A fourth was immature and without spores, and the fifth a pycnidium with subglobose to broadly ellipsoid, hyaline conidia 3·5–4·5 × 2–3·5 μm; no conidiogenous cells could be found. The sixth sporocarp was left unexamined for future investigators. Representative slides from the sporocarps examined are preserved in IMI.

In view of these observations, it is clear that Allescher's taxon was based on discordant elements, the two fungi found by me and a third, perhaps *Phoma cytospora*, with conidia approximating to the shape and width he indicated. This name cannot be satisfactorily typified by these disparate elements and must consequently be rejected.

Pleurosticta lichenicola Petrak, *Kryptog. Forsch.* **2**(2) : 190 (1931).

This new genus and species was introduced by Petrak (*loc. cit.*) for what he interpreted as a lichenicolous coelomycete growing on *Parmelia olivacea* (L.) Ach. in Germany. The identity of this taxon has been investigated by Santesson (1949 : 142) who found it to be based on the normal pycnidia of a different lichen, *P. acetabulum* (Necker) Duby. Unfortunately the type collection could not be re-located in W (H. Riedl, *in litt.*), but there seems to be no reason to question Santesson's interpretation.

Pleurosticta Petrak must consequently be treated as a further synonym of *Parmelia* Ach. nom. cons. Further, as Art. 59 specifically excludes lichenized fungi, if the

group of brown *Parmelia* species for which Esslinger (1978) introduced the new genus *Melanelia* Essl. are regarded as generically distinct, then *Pleurosticta* would be an earlier name for that genus unless conserved, as proposed by Esslinger (1980).

Pseudodiplodia lichenis Vouaux, *in* Bouly de Lesdain, *Rech. Lich. Dunk., Suppl.* : 167 (1914).

Type: France, Malo Terminus, on a telegraph pole, 28 August 1910, *M. Bouly de Lesdain* (herb. Vouaux—holotype!).

Stagonopsis lichenis (Vouaux) Keissler, *Rabenh. Krypt.-Fl.* **8** : 586 (1930).

This species was described as a fungus occurring on *Lecanora saligna* (Schrader) Zahlbr. (syn. *L. effusa* (Hoffm.) Ach.), and has pale orange, cupuliform pycnidia 100–200 μm wide evenly distributed over a greyish-green crustose thallus; the hyaline conidia are curved with rounded ends, 0–1 septate, and $8–10 \times 2–4$ μm. No *Lecanora* apothecia were found on the specimen. The lack of damage to the host as well as the even distribution of the pycnidia on the thallus leave no doubt that this name was based on the pycnidial state of an unidentified lichenized fungus. The shape of the conidia recalls that characteristic of the *L. dispersa* (Pers.) Sommerf. group within *Lecanora,* but the orange pycnidia are atypical for that facies.

Vouaux's name was transferred to *Stagonopsis* by Keissler (1930 : 586) primarily because the conidia could be 1-septate.

Pyrenochaeta collematis Vouaux, *in* Bouly de Lesdain, *Rech. Lich. Dunk.* : 275 (1910).

Type: France, Dunkerque, Bray Dunes, on apothecia and thalli of *Collema tenax* (Swartz) Ach., *M. Bouly de Lesdain.*

This fungus was originally described as forming black, almost superficial pycnidia 100–150 μm diam, with 3–9 setae $40–60 \times 3–5$ μm arranged around the ostiole, and producing hyaline simple conidia $5–6 \times 2$ μm on conidiogenous cells $6–7 \times 1{\cdot}5$ μm. Vouaux (1912 : 185, 1914 : 288) suggested that it might represent an anamorph of *Nectria tenacis* (Vouaux) Vouaux, but it would be remarkable for any *Nectria* to have a coelomycete state; *Pyrenochaeta* de Not. species have teleomorphs in *Herpotrichia* Fuckel. As Bouly de Lesdain's herbarium was destroyed in 1940, and this taxon is not represented amongst the remnants of Vouaux's herbarium (Rondon, 1970), it has not been possible to examine any material of this taxon. According to Vouaux's description this fungus cannot have been a *Pyrenochaeta* because the conidiogenous cells in this genus are arranged in long acropleurogenous chains (Schneider, 1979).

Rhabdospora antarctica Speg., *An. Mus. nac. B. Aires* **20 :** 390 (1910); as 'n.f.'

Type: Antarctic Islands, South Orkney Islands ['Nuevas Orcadas'], on *Caloplaca regalis* (Vainio) Zahlbr., February 1908, *C. Spegazzini* (LPS 11231—holotype!).

The host, originally indicated to be a *Teloschistes* Norman species, proves to be the ubiquitous antarctic polymorphic *Caloplaca regalis* (syn. *Polycauliona regalis* (Vainio) Hue). In the original description of this fungus the 'perithecia' were given as black and 75–90 μm diam, and the spores as hyaline, 1-septate or simple, 'rotundato-subtruncatae' and $12–16 \times 2–3$ μm. The holotype is very small, the host fragment measuring only 3×2 mm, but two sporocarps recalling Spegazzini's description were present; one was examined and found to be the pyrenomycete *Polycoccum rugulosaria* (Lindsay) D. Hawksw., which is confined to this host and described and illustrated elsewhere (Hawksworth *in* Pegler *et al.,* 1980). A few of the normal pycnidia of the *Caloplaca* were also found but they form conidia quite unlike those described by Spegazzini (*loc. cit.*). It is consequently clear that *Rhabdospora antarctica* should be treated as a synonym of *P. rugulosaria.* That Spegazzini gave the spores as hyaline and sometimes simple, and also only 2–3 μm wide,

indicates that he based his description on some immature ascospores. Neither asci nor conidiogenous structures were mentioned by Spegazzini.

The name *Rhabdospora antarctica* was evidently missed by Vouaux (1914); as a result it seems to have been overlooked by subsequent students of the lichenicolous fungi (e.g. Clauzade & Roux, 1976).

Rhabdospora lecanorae Vouaux, *in* Bouly de Lesdain, *Rech. Lich. Dunk., Suppl.* : 167 (1914).

Type: Spain, Catalogne, Hostaleto, nr Figueras, on *Lecanora chlarona* (Ach.) Nyl. on olives, 11 April 1905, *F. Héribaud* (herb. Vouaux—lectotype!).

In Bouly de Lesdain's publication three collections were cited, on *Opegrapha vulgata* (Ach.) Ach. (syn. *O. cinerea* Chev.) from Dunkirk, on *Micarea nitschkeana* (syn. *Bilimbia spododes* (Nyl.) Arnold) thalli from Bergues, and on *Lecidella elaeochroma* (Ach.) M. Choisy (syn. *Lecidea parasema* auct.) from Ghyvelde. Vouaux's selection of the epithet *'lecanorae',* however, implied that he had a fourth collection in mind when providing his description for Bouly de Lesdain, on *Lecanora.* Vouaux (1914 : 290) cites a collection on *L. chlarona* first, before the Bouly de Lesdain material, and this must be regarded as a syntype for this name. As only this latter collection is extant it is here designated as the lectotype.

The type is in a poor condition and is overgrown by superficial moulds; in some apothecial margins acicular to arcuate or sigmoid hyaline conidia 20–30 × 1–1·5 (–2) μm, produced on pyriform conidiogenous cells 4–6 × 3–5 μm, were found. Identical conidia were also produced in black pycnidia directly on the thallus, something overlooked by Vouaux. These correspond to the pycnidia (spermogonia) usually produced by this lichen, and the name *Rhabdospora lecanorae* should consequently be treated as a synonym of *Lecanora chlarona.*

Rhabdospora lesdainii Vouaux, *Bull. trimest. Soc. mycol. Fr.* **30** : 290 (1914).

Type: France, Malo-Terminus, on *Lecidella elaeochroma* (Ach.) M. Choisy (syn. *Lecidea parasema* auct.) on *Populus monilifera, M. Bouly de Lesdain.*

The type material is not amongst the remnants of Vouaux's herbarium (Rondon, 1970), and as that of Bouly de Lesdain was destroyed in 1940, must be presumed lost. The fusiform, straight to slightly curved conidia were described as with 5–7 'plus ou moins distinctes' septa and given as 38–60 × 3–4·5 μm. The normal conidia of this species recall Vouaux's description of their shape but are not septate (only guttulate) and only 17–18 μm long (Galløe, 1927 : 92). The name is consequently of uncertain application.

Rhabdospora thallicola Tassi, *Bull. Lab. Orto Bot. Reale Univ. Siena* **3** : 129 (1900).

Type: Brazil, 'corteccie di Cinchona', September 1900, herb. F. Tassi (SIENA—holotype!).

The type collection comprises two pieces of bark each covered with the creamy-white thallus of a sterile crustaceous lichen. The pycnidia are scattered rather regularly over the material and not associated with any signs of damage. The filiform conidia and arrangement of the conidiogenous cells is similar to that seen in the pycnidia of numerous lichens, particularly the *Lecanora chlarotera* Nyl. group. This name is consequently excluded as based on the pycnidia of an unknown lichen.

Sphaeromma mazosiae Upadhyay, *Publções Inst. Micol. Recife* **402** : 4 (1964).

Type: Brazil, Rondônia, Porto Velho, Perfil AR-4, on *Mazosia melanophthalma* (Müll. Arg.) R. Sant. on *Orbigyna martiana,* January 1962, *O. M. Fonseca* (URM 38672 [19.945 p.p.]—holotype!).

The herbarium specimen URM 19.945 comprises twelve portions of leaf, mostly about 10–12 cm long, which support a wide range of lichens and associated lichenicolous fungi constituting 'Fungos do Brasil' nos. 38670–38682 (i.e. including the holotypes of both *Sphaeromma mazosiae* and *Sporhaplus rondoniensis* Upadhyay). *Sphaeromma mazosiae* and *Sporhaplus rondoniensis* were both described as having superficial, dark brown pycnidia (33–45 μm diam and 30–35 μm diam, respectively) with stout, dark brown setae (given as 6–12·5 × 3·4 μm for *each* species); the *Sphaeromma* was stated to have 2–4 septate conidia 7–10·5 × 1·5–2 μm, and the *Sporhaplus* simple conidia 1·5–2 × 0·75–1 μm. Only after very extensive searching did I manage to locate any *Mazosia* thalli with setose sporocarps recalling those of the original description; several of these were squashed and found to contain pseudoparenchymatous tissue, young asci, or asci with 1-septate hyaline immature spores about 8 × 4 μm. It seems probable that the ascomycete is identical to the monotypic *Keratosphaera batistae* Upadhyay, the holotype of which (URM 38673) should be on this specimen, although its spores were indicated to become 3-septate when mature and measure 6–10 × 2–2·5 μm, and no evidence for the existence of paraphyses figured by Upadhyay (*loc. cit.* : 10) was obtained.

The host lichen was originally referred to *Mazosia phyllosema* (Nyl.) Zahlbr. by Upadhyay, but the thallus is not smooth but has the minute whitish verrucae characteristic of *M. melanophthalma* (Müll. Arg.) R. Sant., although they are rather poorly developed in this material. According to Santesson (1952 : 118), *M. melanophthalma* has macroconidia 5–8 × 2–3 μm and microconidia 2–3 × 1 μm; the correspondence between the sizes of these and those given for *Sphaeromma mazosiae* and *Sporhaplus rondoniensis* is striking. In my opinion descriptions of both these fungi were probably based on the conidia of *M. melanophthalma* (the 'septation' of the larger conidia being due to guttulation) and sporocarps of the *Keratosphaera*. These two names cannot consequently be satisfactorily typified and must be rejected.

Sphaeronema lichenophilum Durieu & Mont., *in* Montagne, *Syll. gen. crypt.* : 249 (1856).

Type: Algeria, 'sur les troncs du vieux *Chamaeropis*, du Marabout du sommet du Bouzaréah', 8 April 1844, *M. C. Durieu de Maisonneuve* (PC—holotype!).

This name has generally been cited as first published in *Botanique I. Cryptogamiae* of Durieu's *Exploration scientifique de l'Algérie,* which is referred to with correct page numbers in Montagne's book cited above. However, it is now clear that the part of Durieu's work including *Sphaeronema lichenophilum* lay in proof for at least 13 and perhaps as many as 23 years before they were finally published in October 1869 (Hawksworth & Booth, 1974 : 12); only the first parts of this volume were issued in 1846–50, the dates usually given for *S. lichenophilum.* Montagne cited only the single collection detailed above, which is consequently the holotype; Durieu mentioned the same collection, but also a further one made on *Chamaeropis* in February 1840 which is also now preserved in PC (!).

Durieu gave the host as '*Lecideae canescentis* aut *Dirinae Ceratoniae*', but in the holotype, the 1840 specimen, and further two small undated specimens in PC (!), the pycnidia are distributed over a whitish-grey, thin, crustose thallus forming circular patches mainly 5–10 mm diam. Eleven fragments of bark comprise the holotype sheet, ten of which have pycnidia conforming to the original description, but the other is *Diploicia canescens* (Dickson) Massal. unaffected by any pycnidia. In vertical section the pycnidia were found to extend down through the thallus to the bark and this, together with their even distribution and no evidence of damage to the thallus, strongly suggest that they are the pycnidia of a lichenized fungus, and not an independent coelomycete invading a lichen. The pycnidia are thick-walled, dark brown and carbonaceous, perennial with new pycnidia arising within effete ones, phialides mainly about 10 × 1·5 μm, and numerous, minute, simple, cylindrical, guttulate conidia mainly

5–6 × 2–3 μm. Its identity is uncertain, although the pycnidia suggest Arthoniales or Hysteriales; it is not *Dirina ceratoniae* Fr., the pycnidia of which were illustrated by Vobis & Hawksworth (1981).

Sphaeronema lichenophilum was also very tentatively reported from a *Parmelia* collected in 1921 in Brazil (São Paulo, Prémembé) by Keissler (1933 : 385), but as the material was stated to be in Bouly de Lesdain's herbarium it was presumably destroyed in 1940.

Sphaeropsis cladoniae Ell. & Ev., *J. Mycol.* **5 :** 149 (1889).

Coniothyrium cladoniae (Ell. & Ev.) Sacc., *Syll. Fung.* **10 :** 268 (1892).

Lichenoconium cladoniae (Ell. & Ev.) Petrak & H. Sydow, *Beih. Rep. nov. Spec. Regni veg.* **42 :** 433 (1927).

This name was based on a collection including an *Abrothallus* species and *Lichenoconium usneae,* but is considered correctly used for the former element (Hawksworth, 1977 : 192–193).

Sphaeropsis scripta Schwein. ex Berk. & M. A. Curtis, *J. Acad. nat. Sci. Philad.* **2 :** 280 (1853).

Dothiorella erumpens Sacc., *Syll. Fung.* **3** : 242 (1884); as '(Berk. & C.)', nom. illegit. (Art. 63.2).

This fungus was listed as a lichenicolous species by Viégas (1961 : 869, as '*Dothiorella erupens*' [sic]) but Berkeley & Curtis (*loc. cit.,* pl. 25 fig. 3a–*c*) illustrated a black, stromatic, pulvinate, multilocular conidioma bursting through the bark from below, and were evidently not dealing with a lichenicolous fungus; the fungus was erumpent through unidentified lichens on the bark, not on the lichens themselves. The conidia of the fungus were broadly ellipsoid, hyaline, simple, with a short persistent pedicel.

Spilomium epicladonia H. Olivier, *Paras. Lich. Fr., Suppl.* : 22 (1907) [not seen].

Type: France, Hérault, Mons-la-Frivola, on *Cladonia* sp., *A. de Crozals.*

No type or authentic material of this taxon has been located. Vouaux (1914 : 198) considered it might be identical to the species now called *Bachmanniomyces uncialicola,* but this seems unlikely to be correct (see p. 14).

Sporhaplus rondoniensis Upadhyay, *Publções Inst. Micol. Recife* **402 :** 7 (1964).

Type: Brazil, Rondônia, Porto Vehlo, Perfil AR-4, on *Mazosia melanophthalma* (Müll. Arg.) R. Sant. on *Orbigyna martiana,* January 1962, *O. M. Fonseca* (URM 38674 [URM 19.945 p.p.]—holotype!).

The holotype of this monotypic genus is present on the same collection as that of *Sphaeromma mazosiae* and some other fungi, and is discussed under *S. mazosiae* above (p. 86).

Sporocadus lichenicola Corda, *Icones Fung.* **3 :** 24 (1839).

Type: Czechoslovakia, Prague, Fürstl. Lobkowitzischen Garten, on *Rosa* sp., 1838, *A. J. C. Corda* (PRM 155664—holotype n.v.).

Hendersonia lichenicola (Corda) Fr., *Summ. veg. Scand.* **2 :** 416 (1849); as '(*Sommerf.*)'.

Seimatosporium lichenicola (Corda) Shoem. & E. Müller, *Can. J. Bot.* **42 :** 405 (1964).

This taxon, the lectotype species of the generic name *Sporocadus* Corda (Hughes, 1958 : 810), was thought by Corda to be associated with some unidentified crustose lichen because algal cells were associated with the pycnidia of the fungus below the surface of the host. The type material was examined by Hughes (*loc. cit.*) and his slides were also studied by Shoemaker & Müller (1964); these, together with numerous later collections identical to Corda's species, demonstrate conclusively that this is not a lichenicolous fungus, but rather a common saprophyte of *Rosa* stems. The algae present in

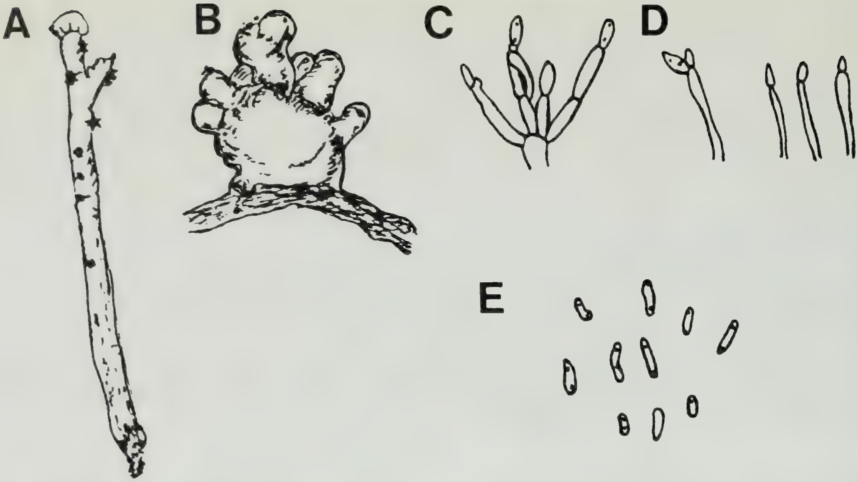

Fig. 36 *Verrucaster lichenicola.* **A,** Infected podetium (× 2). **B,** Gall with pycnidia (× 12). **C,** Conidiophores (× 1000). **D,** Conidiogenous cells (× 1000). **E,** Conidia (× 1000). Reproduced from Tobler (1913 : 383).

Corda's collection occurred only fortuitously. Corda's fungus is correctly placed in *Seimatosporium* and has an extensive synonymy (Sutton, 1975 : 136); it is the anamorph of *Clathridium corticola* (Fuckel) Shoem. & E. Müller (syn. *Griphosphaeria corticola* (Fuckel) Höhnel) the connection between the two having been demonstrated by cultures of the ascospores giving rise to the *Seimatosporium* state (Shoemaker & Müller, 1964).

In accepting '*Hendersonia lichenicola*' as a lichenicolous species, Clauzade & Roux, 1976 : 89) were presumably simply following Keissler (1930 : 578) who listed it from several lichen hosts; these must be presumed to be cases where the fungus grew through overlying lichen thalli or otherwise they were misidentifications.

Sporocadus rosicola Rabenh., *Bot. Ztg* **6** : 294 (1848); as '*rosaecola*'.

Type: Germany, prope Leipzig, 'ad Rosarum ramulos', *L. Rabenhorst* [*Fungi Exs.* no. 66] (not seen).

Rabenhorst's fungus occurred on *Rosa* branches and there can be little doubt that its usual treatment as a synonym of *Seimatosporium lichenicola* (Corda) Shoem. & E. Müller is correct (Sutton, 1975 : 136). However, Saccardo (1884 : 439) stated that it had been found '. . . in apotheciis *Lecideae luteolae* [i.e. *Bacidia rubella* (Hoffm.) Massal.], Gand in Belgio'. This later report must be treated as a misidentification based on an unknown lichenicolous fungus.

Verrucaster lichenicola Tobler, *Abh. naturw. Ver. Bremen* **21** : 384 (1913) ['1912']. (Fig. 36A–E)

Type: Germany, Oldenburg, Kehnmoor, on *Cladonia bacillaris* auct., *H. Sandstede.*

This new genus and species was introduced by Tobler (1913) for a fungus forming gall-like growths on podetia of the host. The pycnidia were described as superficial, and opening irregularly, waxy, forming simple, hyaline, narrowly ellipsoid 2-guttulate conidia 3·6–7·6 × 0·8–1·6 μm from elongate conidiogenous cells apparently arranged on short conidiophores (Fig. 36C–D). The material on which this taxon was based has not been located in B (B. Hein, *in litt.*) or MSTR (B. Gries, *in litt.*); cryptogam collections in BRM are currently unavailable during re-housing (H. Kuhbier, *in litt.*), and any at DR would have been destroyed in 1945 (F. Mattick, *in litt.*).

The galls produced by this fungus recall those of *Epicladonia sandstedei* (see p. 16), but the waxy, superficial pycnidia, and the simple and much narrower conidia, make it unlikely to belong there. *Bachmanniomyces uncialicola* is easily excluded as a possibility on the basis of conidial shape (p. 11), and *E. simplex* (p. 19) by the much shorter and narrower conidia.

As I have seen no fungus recalling Tobler's description in all details, the application of his name must currently remain uncertain. However, the possibility that Tobler was dealing with an *Epicladonia* species cannot be entirely discounted.

Acknowledgements

Without the important studies of Dr B. C. Sutton on generic names and generic concepts in the Coelomycetes as a whole the present investigation would have been impossible. I have also benefited from his comments as to the placement of various taxa treated in this work, but stress that the decisions taken are my own. I have also continued to receive a steady stream of enigmatic specimens from Mr B. J. Coppins, which not only led to the discovery of some hitherto unrecognized taxa, but further enabled species concepts to be clarified through the study of more than single collections.

Any revision of this type is heavily dependent on the availability of material from other herbaria. I am indebted to the curators and directors of all herbaria cited in the text (see p. 5) for enabling me to study collections in their care, and further to the following for assistance in trying to locate particular specimens: T. Ahti, S. Chiesa, B. J. Coppins, B. Gries, M. Guerlesquin, B. Hein, H. Hertel, H. Kuhbier, F. Lona, R. Moberg, J. Mouchacca, U. Passauer, H. Riedl, Y. Rondon, L. Tibell and O. Vitikainen.

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Host index

Names of lichen-forming fungi mentioned in the introductory sections and elsewhere are also included here. Accepted names are in roman and synonyms in *italic*.

Fungus index

In addition to synonyms cited in this revision, this index contains some synonyms of accepted species for which further information is provided in papers cited in the text. New taxa, and the page numbers of the principal references to accepted species, are printed in **bold,** accepted names in roman, and synonyms in *italic* type. An asterisk (*) indicates pages on which there is a figure.

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Peter S. Dixon & James H. Price

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The genus *Callithamnion* (Rhodophyta: Ceramiaceae) in the British Isles

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Synopsis

The algal genus *Callithamnion* is represented in the British Isles by 10 species: *C. byssoides, C. corymbosum, C. decompositum, C. granulatum, C. hookeri, C. roseum, C. sepositum, C. spongiosum, C. tetragonum* and *C. tetricum*. There is one new combination: *C. sepositum* (Gunnerus) P. Dixon & J. Price.

A critical description is provided for the genus and for each species, together with comments on those features of structure and reproduction of systematic importance, detailed analyses of the validity of these features for taxonomic distinction, and the range of variation encountered in the British Isles and in adjacent regions. A general key to the British species is provided, together with details of the typification of all entities relevant to a consideration of the genus in the British Isles.

Introduction

The genus *Callithamnion* presents a supreme example of the taxonomic confusion in red algae. The following are the principal reasons for this:

1. A lack of understanding of the effects of the environment on an extremely 'plastic' phenotype, capable of variation at many different levels.
2. The lack of data on the extent of that morphological variation and its relation to the limits of subsidiary taxa in different geographical areas.
3. The misunderstanding, misinterpretation and confusion in the application of names at different times, by different workers, in different countries.

The present paper is the beginning of an attempt to rationalize treatment of this group of algae, in terms of morphology, development, variation and systematics.

Our basic orientation has been towards those entities occurring on or reported from British shores. As a result of carrying out typifications and dealing with doubtful reports and records, it became necessary to refer to entities from elsewhere, mostly in western Europe but also in other parts of the Atlantic and Mediterranean. Since the geographical confines of this study were envisaged originally as being from North Cape to the Algarve, with treatment of the genus in full to be undertaken only for the British Isles, data on *Callithamnion* in areas outside Great Britain and Ireland have been considered only in so far as they affect the situation in the British Isles. Treatment of the genus in those areas outside the British Isles is, therefore, not complete.

Aspects of structure and reproduction

The thallus in species of *Callithamnion* is of uniseriate filamentous construction, although this may become obscured through the development of 'cortication'. Each uniseriate filament results from the activity of a single apical cell which divides transversely or obliquely. Once formed, a product cell does not divide again in the plane in which it was produced, so that the number of cells in an undamaged filament is a reflection of the number of divisions of the apical cell. Cells may be uninucleate or multinucleate when mature and, apart from rhizoidal cells, each contains several pigmented chloroplasts. The shape and number of chloroplasts are modified by age or the conditions in which the thallus is growing. Although a product cell does not divide again in the plane of division in which it was formed, it frequently does divide once more in a different plane to form the primordium of a lateral branch. Each primordium is clearly of lateral origin, although the final disposition of branches may appear dichotomous if evection occurs.

Each thallus in *Callithamnion* is thus a complex pattern of filaments. A few filaments are of unlimited or unrestricted growth, whereas most are of limited or restricted growth. The difference between these two types is of a physiological nature, with few easily-definable morphological differences. Interconversions can occur, although for many species there are characteristic arrangements of filaments of limited and unlimited growth. In certain species, other lateral filaments may form which grow downward, investing axes, to form the 'cortication'. These 'corticating' filaments are composed of pigmented cells and they arise

from the basal poles of axial cells or from the lowermost cells of lateral filaments. The latter cannot be clearly distinguished from 'corticating' filaments as either can readily give rise to the other. Nevertheless, the term 'corticating filament' has utility in indicating function and position at that time. The extent of cortication varies considerably, even within and between individuals of the same species.

Following the formation of lateral primordia, cells undergo considerable enlargement so that the volume of mature cells may be as much as 50,000 times the original volume. This enlargement is almost entirely in the basal region of a cell, so that in the mature state the lateral filament is attached at the apical pole. Enlargement is associated with development of a large central vacuole and as a result the cytoplasm becomes a peripheral lining within the wall. Cell size varies considerably, not only with respect to age but also to environmental modifications caused by temperature, light intensity, light quality and photoregime. There are characteristic patterns of variation in cell size due to interactions between laterals and the axes on which they are borne. In some species of *Callithamnion* this is shown most clearly in cells at the base of lateral filaments. These cells are older than cells further along the lateral filaments so that they should be larger, but their smaller size indicates that some retardation of enlargement has occurred, possibly through proximity to the axial filament. There may be other factors involved, since a similar phenomenon occurs in main axes (cf. Dixon, 1971; Price, 1978).

A thallus is attached to the substrate by multicellular rhizoidal filaments which resemble 'cortication' but differ in that pigmented chloroplasts are absent. Such filaments also occasionally develop from the cortication as adventitious outgrowths (Price, 1978). When spores germinate, they divide into an upper and a lower cell, the latter forming only the primary rhizoid. Subsequently, additional rhizoids are formed, initially from the lowermost cells of the axial filament and then from the lowermost cells of lateral filaments.

This discussion of the developmental morphology of *Callithamnion* may at first sight appear to differ markedly from the descriptions given in recent years by various French workers. These use an elaborate system of nomenclature first proposed by Chadefaud (1954; see also 1979). In its original form, this system carried the implication that morphological categories were rigidly distinct one from another, although in recent publications by L'Hardy-Halos (1970, 1971*a, b, c*) a more flexible interpretation has been adopted which we consider relates better to the realities of morphogenetic plasticity in Florideophyceae. This is not the place for a detailed analysis of the French system, and the reader is referred to the publications cited for its details. It seems to us that, with few exceptions, the differences of opinion between the system which we have used and the French system are now largely semantic.

In its vegetative morphology, *Callithamnion* resembles some other genera of the Ceramiaceae, from which it differs in reproductive details. *Callithamnion* and its immediate allies, the '*Callithamnion*-Gruppe' of Kylin (1956), are characterized by the lateral intercalary position of procarps. After fertilization, the support cell divides to produce an auxiliary cell. Once contact has been established with the carpogonium, the auxiliary cell gives rise to gonimoblast initials. These form the filaments of the carposporophyte; the latter may be single and entire or deeply lobed. In either event, each cell of the gonimoblast develops into a carposporangium which produces a single carpospore.

Various other types of spores occur in the genus. Tetrasporangia are probably of the widest occurrence. Structures producing more than four spores have been described and these appear to be parasporangia (cf. Drew, 1939), while structures producing only two spores have been observed. Claims for the occurrence of mature, functional monsporangia cannot be substantiated. For comments on polysporangia, see p. 106.

Analysis of character validity: adult material

1. Main axis characters

The characteristics of main axes demand careful examination to ensure that the structure

under investigation *is* the main axis. Major branches may resemble the primary axis but the identity should not be assumed without question. Analysis of main axis characteristics requires a whole thallus, but herbarium specimens of *Callithamnion* are not always complete. Thalli were often 'pruned' to produce a specimen with a greater aesthetic appeal, while thalli occurring on animals are usually stripped from the substrate during either collection or preservation and thereby often damaged.

(*a*) *Integrity of a main axis throughout the thallus*

Many authors have characterized species of *Callithamnion* by the degree of distinctness of the main axis, differentiating between species in which a main axis is easily distinguishable and those in which it is not. This feature depends in part on whether branching is obviously lateral, and on the extent to which evection occurs so that the branching is of a more dichotomous aspect. From personal observations, the degree to which a main axis remains identifiable in a species is highly variable and the feature is of little value of taxonomic discrimination.

(*b*) *Degree of cortication of the main axis and major lateral axes*

Virtually all treatments of the genus *Callithamnion* have made reference to cortication. Only rarely has this feature been discussed with any degree of precision or with reference to its variability. Appreciation of the relationship between degree of cortication and environmental factors is a relatively recent development (Boddeke, 1958; Harris, 1962; Price, 1978).

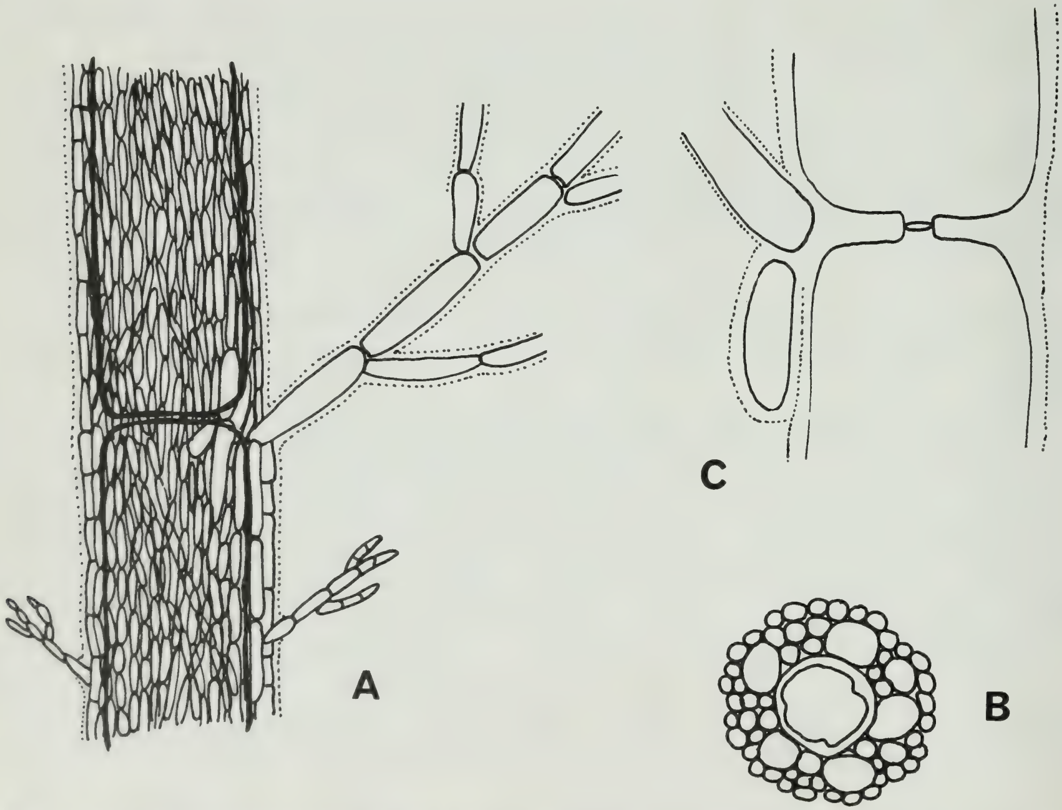


Fig. 1 A, *Callithamnion tetragonum*: a well-corticated axis showing a primary lateral and two adventitious axes arising from the cortication (× 70). B, *C. sepositum*: transverse section of a well-corticated axis (× 35). C, *C. byssoides*: origin of cortication by down-growth from the basal cell of a primary lateral (× 250).

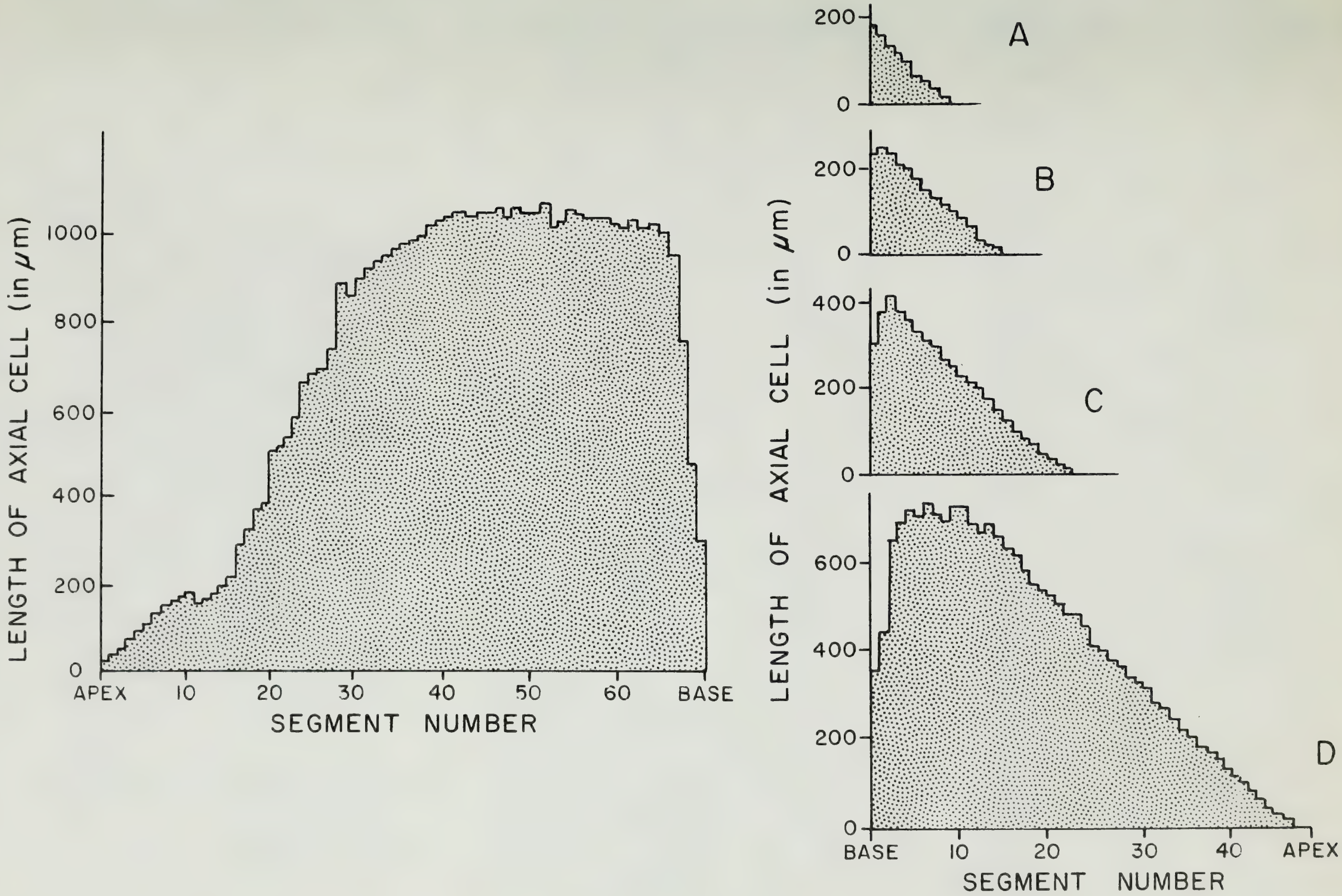


Fig. 2 *Callithamnion corymbosum*: histograms showing cell length along axes. Left: cell length along the principal axis of a small thallus. Right: cell length along primary lateral axes, originating from the 10th (A), 20th (B), 30th (C) and 50th (D) cell of the principal axis shown on the left.

These authors comment that cortical and adventitious development is greatest in entities tolerating or exposed to wave action. This increase in cortication density in such entities appears to result from two causes. There is an increase in the formation of the downward-growing filaments which constitute cortication. Also, without exception, entities occurring in conditions of strong wave action display cells (in the main axis and major laterals) which are short compared with their diameter. As a result, the amount of cortication is increased while the surface area to be covered is less than in an entity where cell enlargement is greater (Fig. 1).

(*c*) *Development of lateral filaments from the cortication*

The down-growing corticating filaments can give rise to adventitious lateral filaments and the occurrence of these has been used by some authors (e.g. Rosenvinge, 1924) to characterize certain entities. Maximum expression of this feature occurs in those entities tolerant of or exposed to severe wave action, where cortication development is greatest. The feature is of little general use as a strictly taxonomic criterion in the genus *Callithamnion* (Price, 1978).

(*d*) *Cell dimensions*

The dimensions or length-to-breadth ratios of cells have been used extensively for discriminating between entities in the genus *Callithamnion* (e.g. Kylin, 1907; Newton, 1931; Boddeke, 1958) even though some authors (e.g. Rosenvinge, 1924) have questioned the value of this feature. It has been demonstrated (Dixon, 1971) that there are elaborate patterns of cell enlargement in species of *Callithamnion*, with regard to both main axes and principal laterals (Fig. 2). Patterns of variation in length-to-breadth ratios are even more complex (Fig. 3). In *Pleonosporium,* which is of similar morphology to *Callithamnion,* variation in cell size has been related to a complex interaction of light intensity and duration (Murray & Dixon, 1972, 1975). There are indications that cell size variation in *Callithamnion* is controlled by similar environmental factors.

The degree of variation in cell size makes it impractical except in certain instances to use this feature for taxonomic discrimination. A further implication of the available studies is that if cell sizes or ratios are quoted for any entity, the positions of the cells measured must be precisely cited. For further detailed consideration, see Price (1978).

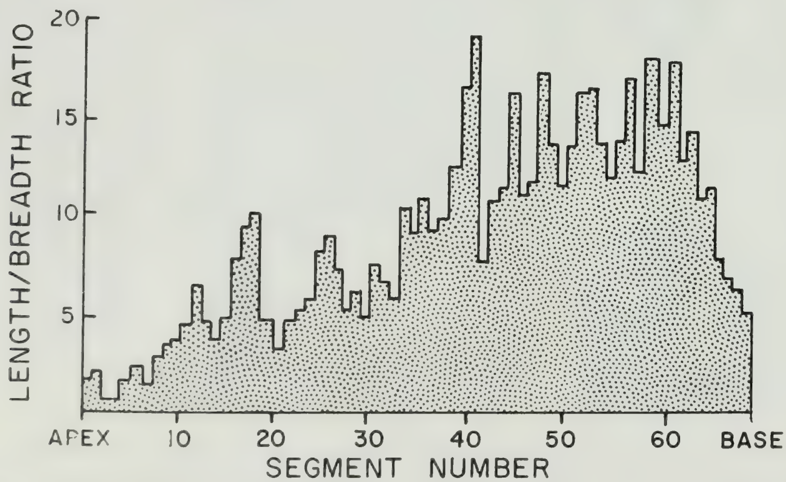


Fig. 3 *Callithamnion corymbosum*: histogram showing the length/breadth ratio of every cell along the principal axis of a small thallus.

2. Characteristics of major laterals

The most important characteristics of the major laterals in the genus *Callithamnion*, from the taxonomic standpoint, are in their branching patterns and arrangement. As previous authors (e.g. Boddeke, 1958; Harris, 1962; Price, 1978) have noted, differences in branching patterns may occur in the same entity in different reproductive states so that the condition of material must always be indicated in discussion of this feature. The arrangement of major laterals in *Callithamnion* is frequently described as 'phyllotaxis', a term not strictly applicable to the algae in the absence of leaves. The alternatives are clumsy or even more inaccurate so that, despite the reservations on its use, we employ 'phyllotaxis' for the arrangement of major laterals.

(*a*) *Branching patterns of major laterals*

Of the several arrangements of filaments that are related to patterns of branching and have been employed in taxonomic discrimination within the genus, two are most significant.

1. The relationship between two individual filaments derived from a common cell lineage; the arrangement may be alternate or pseudodichotomous.
2. The relationship between successive lateral filaments along an axis; these may lie in a single plane (giving a distichous or biseriate arrangement) or be distributed radially (giving a polystichous or spiral arrangement).

Both are potentially useful criteria, although there can be variations in different parts even of a single specimen. Some diagrams illustrating 'phyllotaxis' have been published by L'Hardy-Halos (1970) and more are being prepared for use elsewhere.

(*b*) *Number of orders of laterals distinguishable*

With few exceptions (e.g. *Callithamnion caudatum*), the number of orders of laterals is highly variable depending on a complex of factors, such as the species, the age of the thallus, its vigour and the environment in which it occurs. This feature is therefore of little taxonomic value for specific discrimination.

(*c*) *Reflexion of major laterals*

The tendency of major laterals, particularly of older basal laterals, to be reflexed has been used as a characteristic of certain entities (e.g. Westbrook, 1927). The feature is highly variable and of little taxonomic value.

3. Characteristics of peripheral laterals

The thalli of species of *Callithamnion* are richly branched and the overall form is a reflection of the branching pattern of the constituent filaments. The form of the thallus is determined not only by the arrangement of major laterals, discussed in the preceding section, but also by the arrangements which prevail in the ultimate portions of the constituent filaments. It has become apparent from our investigations that considerable taxonomic dependence can be placed on the morphology, branching pattern and spatial arrangements of what we term the peripheral laterals, so-called because they contribute to the periphery of the thallus. Previous workers with the genus have made extensive use of this feature but, in almost every case, each has used a different term by which to refer to it. A cursory survey of the literature disclosed more than 50 terms which had been applied, of which the most widely used were probably ramuli, ramelli, branchlets, pinnae, and pinnules. The use of different terms, often with variant applications, has produced an impossibly complex terminological situation and it is beyond the scope of the present paper to discuss every usage.

(*a*) *Branching patterns of peripheral laterals*

The branching patterns of major axes can differ markedly from those of peripheral laterals,

such differences often being associated with the formation of reproductive structures. Nevertheless, branching patterns at the peripheral level are usually sufficiently distinct and characteristic for taxonomic discrimination.

(b) Occurrence of 'secund processes'

One particular aspect of the branching pattern of peripheral laterals relates to the occurrence of ultimate lateral filaments which consist only of a single cell. These have been termed 'secund processes' (e.g. Newton, 1931) and used for taxonomic discrimination. Our investigations show that these structures are nothing more than early developmental stages of other organs or laterals.

(c) Overall shape and size

The overall shapes and sizes of peripheral laterals and of their constituent cells have been used by many authors (e.g. Rosenvinge, 1924; Newton, 1931; Feldmann-Mazoyer, 1941) in diagnoses and for discrimination. In our experience, the sizes of entire peripheral laterals are very variable although the shapes and relative sizes of constituent cells are more constant. In addition, other features of a peripheral lateral, such as the number of cells which it contains and its pattern of branching, are particularly significant.

(d) Hyaline hairs

Apical or sub-apical hyaline hairs occur frequently on peripheral laterals in some species of the genus. The function of these structures is unknown and, although widespread, their occurrence and abundance are subject to great variation. A further difficulty preventing the use of these structures for taxonomic discrimination is that they may be damaged or destroyed by fixation or the preparation of herbarium specimens. For further detailed considerations, see Price (1978). Culture conditions may induce or permit the formation of such hairs where field conditions would not. Rosenvinge (1924) found hairs so rarely in *Callithamnion byssoides* (as *C. furcellariae*) that he suggested so distinguishing the taxon from *C. corymbosum;* Rueness & Rueness (1980), by contrast, frequently observed terminal hyaline hairs on female gametophytes of *C. byssoides* in culture.

4. Reproductive characteristics

Reproductive characteristics tend to be relatively stable but the structures are ephemeral and their use as a source of characteristics has been kept to the minimum in this general treatment.

(a) Sporangia

Monosporangia have been reported in various species of *Callithamnion.* Field reports are of immature tetrasporangia, while reports in culture must be dismissed as artifacts so that we have ignored monosporangia for taxonomic purposes.

Bisporangia are produced inconsistently, even in entities where they have been reported, sometimes alone or mixed with tetrasporangia. Their occurrence cannot be relied upon as an absolute criterion. For their significance, see Guiry (1978).

Tetrasporangia are very common and their position, size and shape have been much employed taxonomically in the genus *Callithamnion*, although these characteristics are minimally useful.

A few instances of sporangia containing more than four spores have been detected in British species of *Callithamnion.* These structures can be regarded as parasporangia rather than polysporangia (*sensu* Drew, 1939). The structures are of rare occurrence and the position is confused because *C. decompositum* (which here seems habitually to produce parasporangia as the consistent reproductive structure) has previously been overlooked in

the British Isles (Price & Tittley, 1978). Until it can be confirmed that British *C. hookeri* does produce parasporangia, as in Scandinavia, or does not, their use as a taxonomic distinction is best avoided.

(b) The gametangial phase

Previous authors have made considerable use of structures of the gametangial phase in distinguishing between species. The principal difficulty is that these structures are comparatively ephemeral. For this reason, no attempt has been made to utilize data from the male and female structures or carposporophyte in the present general key. Keys for morphological states other than the vegetative and for ecological characteristics are certainly useful. Keys involving distinctions between the reproductive states of all accepted species will be presented elsewhere (Price, in preparation) although available descriptions are offered in species characterization. As otherwise indicated, periodicity of reproductive structures is less useful and is discussed but not employed.

In the male organs, group distinctions based on the degree of branching in the spermatangiophore system and the positions of spermatangia are reasonably reliable. Positions of the spermatangial clusters and their mature form have also been employed. This is not a new approach; many authors have attempted to utilize these features.

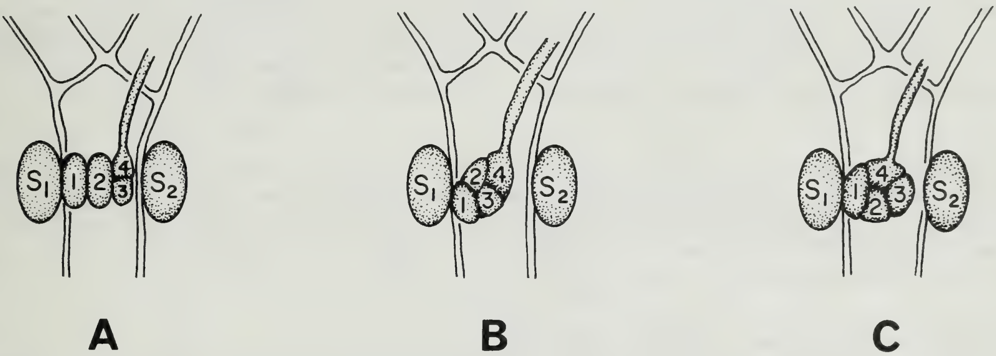


Fig. 4 Cell patterns in the carpogonial branches of different species of *Callithamnion*. A, *C. corymbosum*, B, *C. byssoides*. C, Material identified as '*C. tripinnatum*'. After Miranda (1934). Diagrammatic, not scaled.

The employment of cell spatial arrangements and alignment in the carpogonial branch owes much to observations by Miranda (1934), but has been subsequently developed by other authors. Apart from the ephemeral nature of the material, difficulties of accurate observation of the arrangement of cells precludes use of the data at a principal distinguishing level, but we have employed these data in other contributory capacities. The original concepts put forward by Miranda are shown diagrammatically in Fig. 4; our suggested modifications of or additions to these, with terminological clarification, appear as Fig. 5. Since there is some variation in arrangement and cell relationship, it is highly likely that these aspects of the carpogonial branch depend at least on the relative position of the branch on the thallus, on the bearing support cell, and on the bearing axis. The general position away from functioning apices may reflect the level at which vegetative apical dominance is no longer inhibitory.

Sizes and shapes of carpogonia, trichogynes, and other cells of the procarp all appear too variable to be of taxonomic value at the species level. Trichogyne ramification, not often reported, has been noted by us in a few entities, but its inconsistency suggests aberrations and/or environmental influences. It is possible that different patterns of cell size relationship would emerge for different species from a statistical survey of the carpogonial branch, but the taxonomic utility of this is doubtful.

Fig. 5 Suggested modifications and additions to cell spatial arrangements and alignment types recognized in carpogonial branches by Miranda (1934): variations especially emphasized. (All measurements in μm.) Pp. 109–112.

5A, *Callithamnion tetragonum*, straight form usual to species: Carpogonium width (c/w) 15.
Trichogyne length (t/l) 195.
5B, *C. tetragonum*, intermediate form near zigzag; c/w 7; t/l 99.
5C, *C. tetragonum*, intermediate form near curved: (i) c/w 11; t/l 48; (ii) c/w 9; t/l 64.
5D, *C. granulatum*, zigzag form usual to species: (i) c/w 18; t/l 239; (ii) c/w 18; t/l 71.
5E, *C. sepositum*, curved form usual to species: (i) c/w 18; t/l 75; (ii) c/w 17; t/l–; (iii) c/w 26; t/l 106.
5F, *C. tetragonum*, straight form with extruded 2: c/w 14; t/l 171.

Variations perceived probably depend on relative positions of branch on the axis, on the support cell, and on the overall thallus. They are therefore a reflection of the balance between constraints and overall space available. Types recognized certainly represent arbitrary divisions of a continuum of variation. All figures presented are taken from actual carpogonial branches; dimensions given for the carpogonial width and trichogyne length. Arrows and curves = space relations of cells determined by focal-planing. Symbols: R = bearing axis cells or line of them; S = support cells (S_1; S_2); 1 = cell 1 of carpogonial branch; 2 = cell 2 of c/b; 3 = cell 3 of c/b; 4 = carpogonium with trichogyne.

Straight form
(*Callithamnion corymbosum*-type of Miranda, 1934; 'straight'-type of Harris, 1959, 1962, 1966). Orientation of cells 1 ⟶ 2 usually at right angles to long axis of bearing axial cell (walls of 1/2 therefore parallel to that axis), as in Fig. 5A (example) and Fig. 4A (diagrammatic). Cells 1 ⟶ 2 and 2 ⟶ 3 are in linearly parallel arrangement, carpogonium (4) being variously arranged on 3 (Fig. 5A). Form occurs usually in *C. tetricum*, *C. sepositum*, *C. corymbosum*, *C. roseum*, and *C. tetragonum* (Fig. 5A), sometimes in *C. granulatum*, *C. hookeri*, *C. byssoides* and *C. spongiosum*.

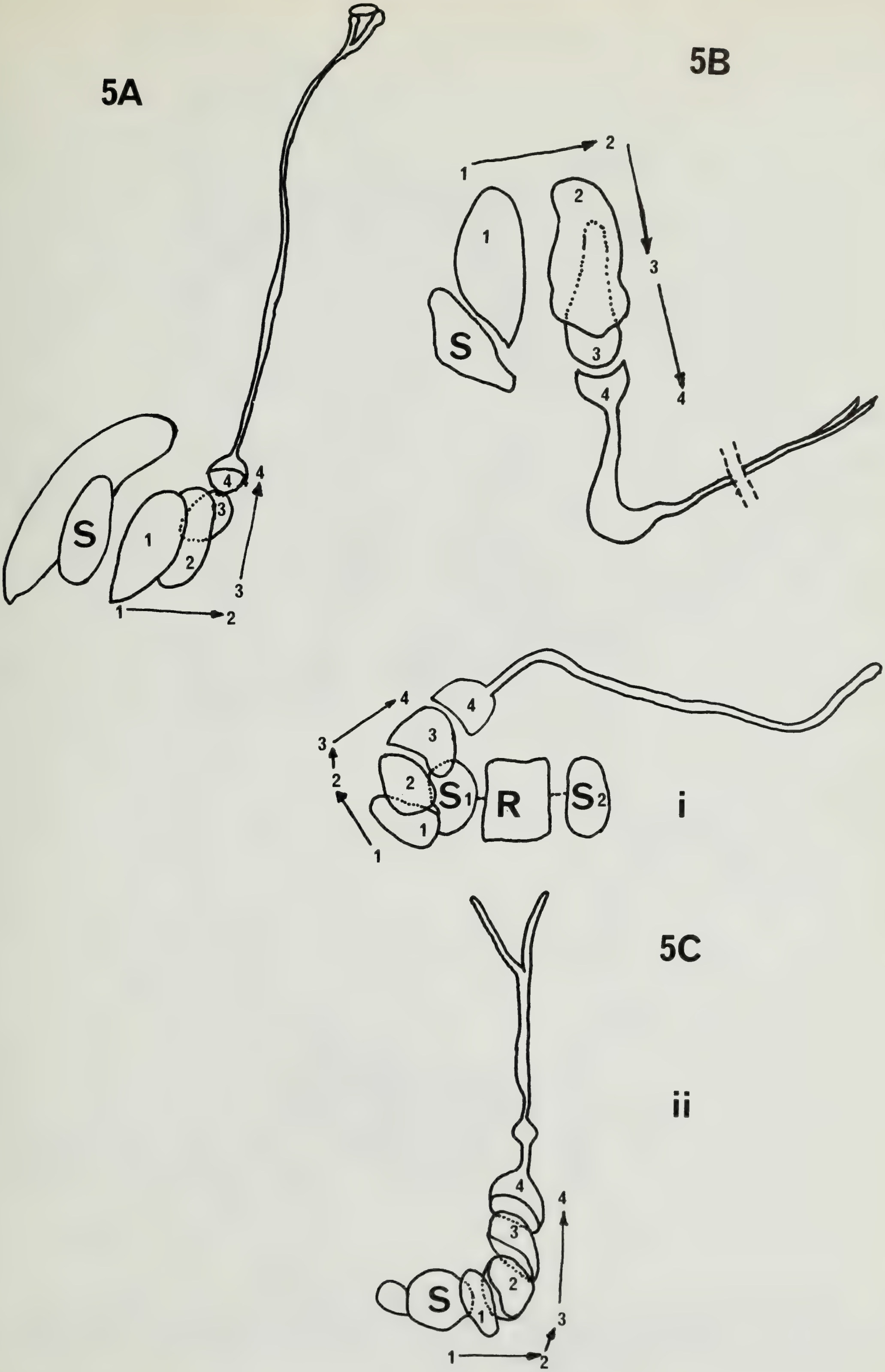
Zigzag form
(*Callithamnion byssoides*-type of Miranda, 1934; 'zigzag'-type of Harris, 1959, 1962, 1966). Compound curve or zigzag (Fig. 4B, diagrammatic). Orientation 1 ⟶ 2 inclined upwards or at outward angle to long axis of bearing axial cell (Fig. 5D). Form occurs usually in *C. byssoides*, and *C. granulatum* (Fig. 5D), sometimes in *C. hookeri*, *C. spongiosum*, *C. roseum*, *C. tetricum*, *C. sepositum*, *C. tetragonum* and *C. corymbosum*.

Curved form
(*Callithamnion* '*tripinnatum*'-type of Miranda, 1934)
Single curve ('U'-shaped), often in more than one plane by lateral curvature (Figs 4C/5E). Form occurs usually (?) in ?*C. tripinnatum*, often in *C. sepositum* (Fig. 5E), and probably sometimes in all known species.

Variations of 'standard' forms
(i). Parallel status of 1 ⟶ 2/2 ⟶ 3 depends on position of pit connexion between cells 2 and 3. If the connexion is high on 3 and 4 (carpogonium) is large or in cramped position, depression or offset position of 3 will cause the relationship

$$\begin{tikzcd} & & 4 \\ 1 \arrow[r] & 2 \arrow[dr] & \\ & & 3 \arrow[uu] \end{tikzcd}$$

to occur (as in Fig. 5B, where 4 (carpogonium) rises towards viewer out of the paper, but would obscure detail if drawn fully so). This is very close to the form attributed by Miranda (1934) to *C. byssoides*-type (Fig. 5D; here in examples of *C. granulatum*).
(ii). If cell 2 is depressed from the 'normal' *C. corymbosum*-type position, and pit connexions 1/2 and 2/3 are high on 2, then the 'U'-shape of Miranda's (1934) '*tripinnatum*'-type is approached, as is usual in *C. sepositum* (Fig. 5E) and occasional in *C. tetragonum* (Fig. 5C).
(iii). Arrangement of the carpogonial branch is not always planar, as is clear from the above and from curvature diagrams accompanying parts of Fig. 5. Angling to the vertical or into more than one plane is common to usual, and can confuse the pattern as, e.g. in Fig. 5F. There, a *C. tetragonum* branch with 1 ⟶ 2 ⟶ 3 all still parallel has 2 extruded by pressure to jut out from the usual line. Otherwise, the branch is clearly of *C. corymbosum*-type (straight), the periphery of the lateral branch system bearing the carpogonial branch being basal to the figure. Harris's (1959, his text-figure 13C) intermediate type may have been due to this non-planar situation.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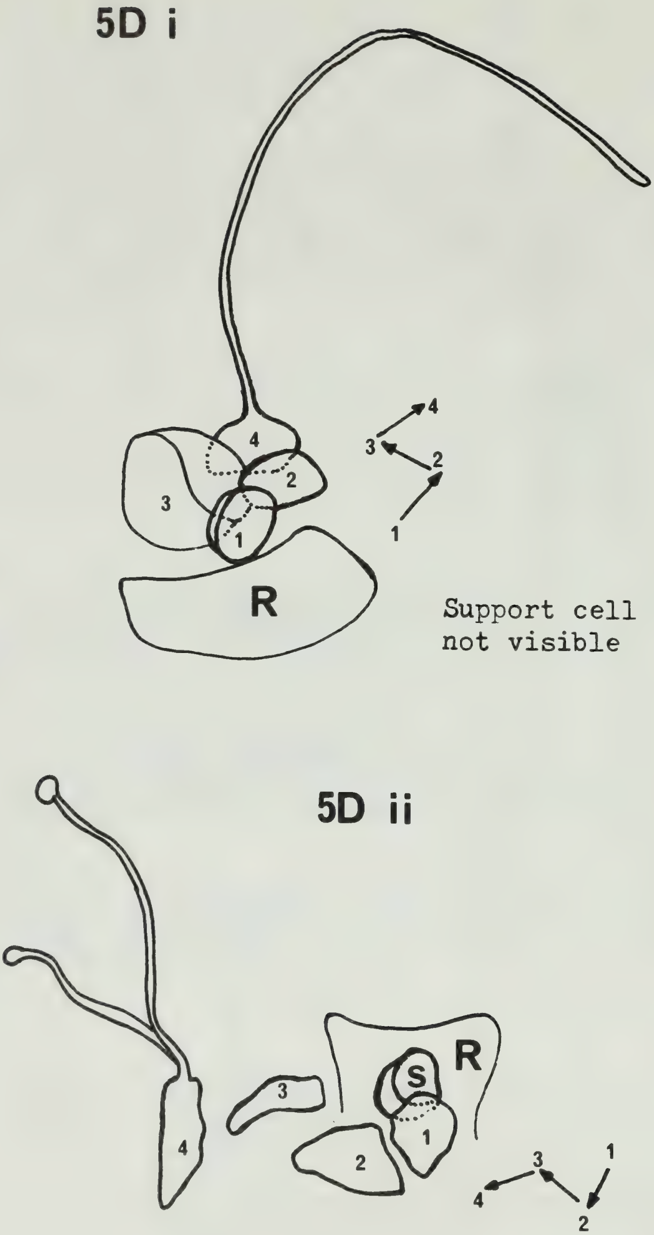
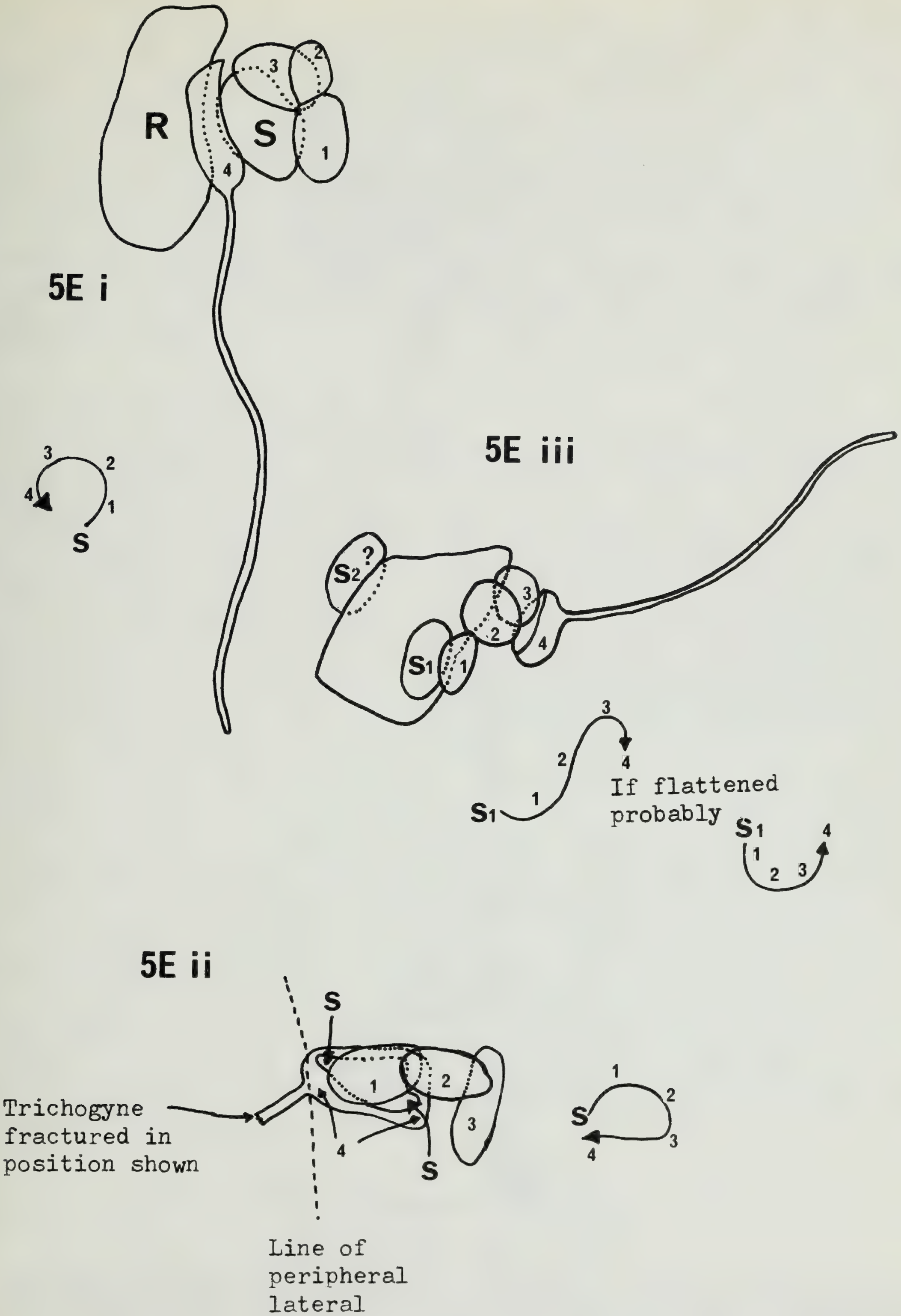


Fig. 5 Suggested modifications and additions to cell spatial arrangements and alignment types recognized in carpogonial branches by Miranda (1934): variations especially emphasized. (All measurements in μm.) Full explanation on p. 108.



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Trichogyne
fractured in
position shown
Line of
peripheral
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2
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3
4

Fig. 5 Suggested modifications and additions to cell spatial arrangements and alignment types recognized in carpogonial branches by Miranda (1934): variations especially emphasized. (All measurements in μm.) Full explanation on p. 108.

(*c*) *The carposporophyte*

Events occurring after fertilization have a standard sequence. It appears that the extent of development and number of cells involved in primary and secondary gonimoblast have a relative constancy that is useful at a contributory level in species distinction. To some extent, basic differences in the early carposporophyte development are reflected in lobing of the carposporophyte at early maturity (carposporangial production). However, subsequent environmental and morphogenetic effects obscure or override the earlier patterns and produce variations in form so that species patterns cannot be distinguished. We have employed such criteria with circumspection in the following treatment. Sizes and shapes of carposporangia and carpospores are of little taxonomic value.

Development of a rudimentary vegetative 'involucre' around the carposporophyte occurs in some of the more delicate species. It is referred to as necessary in the treatments that follow, but it is inadvisable to employ this essentially ephemeral phenomenon as a fundamental criterion.

5. Gross criteria of species and groups

In addition to particular features used as systematic criteria, numerous other gross criteria are cited in diagnoses. Generally, these gross criteria are of little importance and we do not employ them for taxonomic distinction.

Periodicity of upright growth is similar in all species, with one possible exception. It is probable that the less robust forms rarely persist as recognizable basal fragments through the winter, although it is difficult to be sure of that. Robust, exposed shore forms show rather abrupt dieback to variable basal portions in the usual conditions of late autumn or early winter. Those thalli which do persist have lost peripheral or even whole branch systems and, although still recognizable, have a very different appearance from the luxuriant summer growth. One exception, *Callithamnion tetragonum*, tends to persist as recognizable growths on laminae of the Laminariales in some parts of its range. In some years and locations, *C. tetricum* behaves similarly. Although contributory, this behavioural difference is not of prime taxonomic importance.

Statistically, characteristic growth forms can be recognized for most species of *Callithamnion*. Unreliable as primary taxonomic criteria, these are nevertheless very useful. The growth forms are a consequence of growth vigour, robustness, texture, frond outline, branching pattern, and other unquantifiable phenomena. In some species, external form is almost indescribable but still highly characteristic. Species of *Callithamnion* rarely form homogeneous populations with individuals closely-knit enough to possess a recognizable, distinct population morphology. Two species form occasional exceptions to this. *C. roseum* populations mainly manifest what is merely a multiplication of the individual plant characteristics; *C. scopulorum* (now *C. hookeri*) has the most recognizable population morphology that is rather more than merely the sum of many individuals. Many authors have employed the term 'turf' for this. The terms is not entirely satisfactory but it is at least evocative. In northern parts of the British Isles, exposed shore species (principally *C. sepositum*) sometimes grow so densely as to produce what has been equally inaccurately described as 'spongy turf'.

The genus *Callithamnion* Lyngbye

Lyngbye, *Tent. Hydr. Dan.*: 123 (1819).

Phlebothamnion Kützing, *Phyc. Gen.*: 374 (1843).
Poecilothamnion Nägeli in *Neue Denkschr. Allg. schweiz. Ges. ges. Naturw.* **9** (un-nod. Art. 2): 202 (1847).
Leptothamnion Kützing, *Sp. Alg.*: 896 (1849).

Dorythamnion Nägeli in *Sber. bayer. Akad. Wiss.* **1861** (2) : 344 (1862).
Ceratothamnion J. Agardh in *Acta Univ. lund.* **28** (6) : 35 (1892).
Aglaothamnion Feldmann-Mazoyer, *Rec. Céram. Méd. occident.*: 451 (1941).

Thallus of variable shape, colour and size; colour rose-pink to muddy yellow-brown, varying with species, vigour and habitat in natural conditions, between specimens and within a single specimen; size and shape vary with species, specimen and habitat conditions; filamentous, axes uniseriate, to 400 mm in length, variably but always copiously branched; branching monopodial, although some species are peripherally flabellate from pseudodichotomous evection; sometimes corticate by down-growing filaments derived from cells of axis or basal cells of primary laterals, less often from subsequent order laterals; cortical development and extent variable according to species, specimen and habitat conditions, involving main axis only, or all orders of major axes; adventitious branching from cortication in a few species, most dense in exposed shore specimens where a densely interwoven continuous thick matrix is formed over the cortication; axial widths over cortication reaching 5 mm; normal branching alternate, spiral or distichous, or approaching dichotomy in aspect; irregularities occur occasionally in all species, with some variation with reproductive state; characteristic form of the peripheral laterals occurs in both determinate smaller apical or peripheral laterals (commonly referred to as 'ramuli') and indeterminate higher order laterals (in most species), where the latter levels represent the current apices of the branching system and contribute to the form of the thallus periphery; active main apices (main axes and major laterals) either buried within local peripheral lateral development or clearly emerging above that development according to species; apical cells of peripheral laterals gradually- to abruptly-domed cylinders, of variable length according to species, or cones; apical (or subsequently sub-apical) unicellular hyaline hairs irregularly present in active (younger) parts of frond in many species, hairs commonly and often suddenly deciduous; cells length-to-breadth ratios variable within the range 16 : 1 to 1 : 1 for all parts of the vegetative thallus; cells multinucleate with uninucleate immediate products of apical division, or uninucleate throughout, according to species; chloroplasts irregular and/or discoid in young cells, forming irregular masses or ribbons by division and coalescence when older; chromosome numbers commonly variable in the range n = 28–33, with extremes to n = 90–100.

Gametangial thalli commonly dioecious, occasionally monoecious in many species, habitually in one. Spermatangia arise either in separate cushions, formed on cells of outermost peripheral laterals, one or more per cell, cushions sometimes coalescing; or in secund rows on adaxial surfaces of peripheral laterals, spreading when luxuriant to sides and sometimes abaxial surfaces, finally encircling more mature, usually basal, parts; vigorous production of spermatangia may lead to additional development from cells of major branches of all orders in lateral systems, as in *Callithamnion corymbosum* or *C. hookeri*.

Procarps formed normally just behind or near apices of active axes and major indeterminate laterals, but may occur on lower branches in thalli with more vigorous reproductive development; early procarp development with paired support cells, exceptionally with only one, formed laterally on bearing axis; carpogonial branch developing on one support cell or on both support cells, four-celled, including carpogonium; cell arrangement straight, U-shaped, zigzag, or any intermediate of these; carpogonium relatively small, 6·5–26 μm in breadth, but with trichogyne of very variable dimensions and shape, curved, ramified, nodular, swollen, uneven-sided, or bulbous-tipped, 47–242 μm in length; trichogyne degenerating after fertilization, the carpogonium transferring a derivative of the fertilization nucleus by a connecting cell, or directly, to an auxiliary cell formed by division from the original support cell; following nuclear transfer the auxiliary cell dividing to produce a central cell and a foot cell, central cell developing two, less often three, gonimoblast initials, all producing few-celled gonimoblast filaments; one or two lobes of the gonimocarp developing on the ultimate cell of the gonimoblast, one only on the penultimate cell of the gonimoblast and on all subsequent cells; gonimolobes rounded, conical or uneven, varying according to species, environmental factors and state of maturity; carposporophyte very

rarely sheathed by enveloping vegetative filaments; carposporangia of variable dimensions at maturity, commonly 25–70 μm in diameter.

Tetrasporangia ellipsoid or ovoid, less often subspherical to spherical, variable in size and shape to 130 × 120 μm, formed adaxially on cells of peripheral laterals, usually one or two per cell; bisporangia usually exclusively on particular plants (*Callithamnion byssoides*) but sometimes intermixed with tetrasporangia in *C. byssoides* and *C. hookeri*; parasporangia reported elsewhere, not often authenticated in Britain, except in *C. decompositum*.

General key to British species

Price (1978) has correctly indicated that ecology should be the initial approach to a utilitarian key aimed at field use with fresh material. Here, with all the complications of older herbarium or preserved material and sparse ecological data, this is not practicable. Nevertheless in the present key an attempt is made to integrate thallus or population characteristics likely to have been noted or obvious from morphological state even in individuals out of their normal environment. Use is also made of some data of reasonable reliability derived from customary habitat preferences. All these aspects have been utilized by past authors but an integrated key which does not place too much dependence on any one criterion has not been attempted previously. Keys specific to ecology and to reproductive states are being published elsewhere (Price, 1978; Price, in preparation).

1 Laterals of limited growth *not* overtopping bearing axis 2
– Laterals of limited growth overtopping the axis on which they arise 3
2 Cells uninucleate; cortication not commonly (although potentially) giving rise to an interwoven matrix of adventitious laterals; thallus almost never coarse, shaggy, or rope-like . . . . **C. hookeri** (p. 122)
– Cells largely multinucleate; interwoven matrix of adventitious laterals arising from cortication in at least the lower 7/8ths of the thallus; thallus always coarse, shaggy, and rope-like in mature specimens, although less so if sublittoral . . **C. tetricum** (p. 128)
3 Lateral rudiments arising from the first product of a principal apical cell 4
– Lateral rudiments arising on or after the second product of a principal apical cell . . . 8
4 Apical cells of limited growth peripheral laterals rounded terminally into a dome, sometimes strongly tapered 5
– Apical cells of limited growth peripheral laterals very small (12 ± 3 μm long), conical . . . . **C. tetragonum** (p. 127)
5 Cell lengths not exceeding 5 × breadth in any part of the thallus; ramification below lateral branch system level strictly pseudodichotomous or not at all so, never mixed . . . 6
– Cell lengths exceeding 5 × breadth in older axes and major laterals; ramification below lateral branch system level strictly pseudodichotomous . . . **C. corymbosum** (p. 118)
6 Cells uninucleate; interwoven matrix of adventitious laterals from cortication usually absent . . . . **C. hookeri** (p. 122)
– Cell multinucleate; interwoven matrix of adventitious laterals from cortication develops over at least most of main axes and principal laterals 7
7 Apical clusters of lateral systems > 700 μm across; peripheral laterals (containing more than 7 cells) with their greatest width well above their base or parallel-sided for much of their length; ramification pinnate; common on exposed shores in the sector from south Ireland and south Wales northwards round to Yorkshire . . . . . **C. sepositum** (p. 124)
– Apical clusters of lateral systems < 700 μm across; peripheral laterals (containing fewer than 6 cells) with greatest width at or near their base; ramification pseudodichotomous; either rarely recorded anywhere on exposed shores or rare in the north of the British Isles 9
8 Cells multinucleate; cells near apices > 30 μm diameter . . . **C. roseum** (p. 123)
– Cells uninucleate; cells near apices < 20 μm diameter . . . . **C. byssoides** (p. 116)
9 Peripheral laterals with more than three cells above last ramification present in most lateral systems; common on exposed shores in the southern half of the British Isles . . . . **C. granulatum** (p. 120)
– Peripheral laterals with never more than 2 cells, most usually only one cell, per lateral

above last ramification anywhere in the periphery, detailed peripheral branching pattern 'aping' *C. corymbosum*; probably widespread on exposed shores but sparse and rarely authentically recorded . . . . **C. spongiosm** (p. 126)

Note: *C. decompositum* (p. 119) is omitted from this key, although described as fully as possible below. Comparative information does not permit effective keying with so little material available. The presence of parasporangia and strictly distichous apical arrangement indicate that confusion is possible only with *C. hookeri* or *Compsothamnion*. In the forms of *Callithamnion hookeri* in which the indeterminate apices are *not* or only just overtopped by determinate laterals, there is commonly discernible variation somewhere on the plant from the distichy by which many indeterminate branch system apices may resemble those of *C. decompositum*. The tetrasporangia in *C. decompositum* are a mixture of sessile (predominantly) and pedicellate (very occasionally), differing from the consistently terminal tetrasporangia on pedicellate laterals in *Compsothamnion*. The latter is also more delicate and less luxuriantly branched than *Callithamnion decomposition*.

Accepted species

1. Callithamnion byssoides Arnott ex Harvey in Hooker, *Eng. Fl. Sir J. E. Smith*, **5** : 342 (1833).

Callithamnion arnottii Trevisan, *Nomen. Alg.* . . . **1** : 77 (1845)
Callithamnion furcellariae J. Agardh, *Sp. Gen. Ord. Alg.* **2** (1) : 37 (1851).
Callithamnion hiemale Kjellman ex Kylin, *Stud. Alg. schwed. Westk.*: 170 (1907).

The accepted binomial, *Callithamnion byssoides*, may by antedated by two binomials. *Callithamnion arachnoideum* C. Agardh, *Sp. Alg.* **2** (1) : 181 (1828), was described from the American coast of the north Atlantic. Although some American material resembles closely the specimens from the eastern shore of the north Atlantic, further detailed study is needed before conspecificity is accepted without question. *Ceramium tenuissimum* Bonnemaison in *Mém. Mus. Hist. nat. Paris* **16** : 132 (1828), was described from European material, but exact typification of this binomial is not possible (see p. 136).

Thallus of wide colour range, from pink to brick red; to 70 (–120) mm in height, bushy, flaccid, rarely with easily recognizable main axis, although usually only one exists, less often several more or less equivalent major axial branches diverge just above attachment; main axis to 120 (–180) μm in breadth, commonly ecorticate throughout, less often with a few basal, down-growing, corticating filaments from lower branches; axial cells narrowly elongate, length-to-breadth ratios commonly 5 (or more) to 1 with detected range 3·00–13·19 to 1; branching alternate, monopodial throughout, with laterals arising irregularly in direction and number; laterals of variable length in lower thallus, of more even length in upper; uppermost larger laterals and peripheral laterals sparsely or not branched, long, flaccid, flagelliform; insertion appearing distichous in lower regions, but becoming clearly spiral towards apices of branching system; peripheral laterals usually unbranched, borne in proximal 3/4 of bearing penultimate laterals but forming small corymbose or uneven clusters near apices in distal 1/4 of bearing laterals, commonly straight, rarely incurved; apical development in lateral systems not pseudodichotomous, but apical cell surpassed by peripheral laterals; cells of laterals cylindrical, of similar length on the same lateral; apical cells of peripheral laterals elongate domed cylinders, $52·59 \pm 17·17$ μm in length, $12·2 \pm 3·33$ μm in basal breadth and $5·49 \pm 2·24$ μm in apical breadth, with length-to-breadth ratio of (2·5–) 3·5–5·5 to 1; peripheral laterals contain (1–) 2–5 (–7) cells, 51–430 μm in length, 7–26 μm in greatest breadth, with position of maximum breadth usually above base.

Gametangial thalli dioecious. Spermatangiophores once-branched, sometimes with rudiments of second lateral, often several on each cell of peripheral laterals; spermatangiophore branches 4 to 5 cells in length; 1–5 spermatangia on each cell, 6×8 μm, but variable in size.

Procarps formed behind apices of major axes and branches, also spreading towards the base in very fertile material, with two support cells but sometimes only one; carpogonial

branches zigzag or straight, on each support cell, but fertilization usually only unilateral; two gominoblast initials from each auxiliary cell, first-developed producing two-celled primary gonimoblast, second-developed forming one-celled primary gonimoblast, two gonimolobes developing from the apical cell of first-developed primary gonimoblast, with one gonimolobe forming from the subapical cell of first-developed and second-developed primary gonimoblast; gonimolobes not lobed, narrow to pointed when young, becoming rounded when mature, carposporangia 20–35 (–40) μm in length.

Sporangial thalli may bear tetrasporangia or bisporangia (cf. Kylin, 1907; Rosenvinge, 1924), but usually not both, although this was reported by Harris (1959, 1962); bisporangia ellipsoid, $62{\cdot}4 \pm 5{\cdot}7 \times 33{\cdot}4 \pm 5{\cdot}6$ μm, with transverse division; tetrasporangia sub-ellipsoid to sub-spheroid, $55{\cdot}2 \pm 4{\cdot}6 \times 40{\cdot}9 \pm 7{\cdot}4$ μm, with tetrahedral spore arrangement; both usually sessile, tetrasporangia occasionally with 1-celled pedicel, borne adaxially on peripheral laterals of higher order but not prolifically on the smaller laterals of subsidiary axes, usually 1 (–2) per cell.

Thalli with tetrasporangia or gametangia from March to November in the British Isles. The presence of tetrasporangia on gametangial plants (Feldmann-Mazoyer, 1941; Foldvik, 1963; comments in Rueness & Rueness, 1980) or of bisporangia amongst gametangia (Rosenvinge, 1924) has not been detected in British field material so far.

Ecology and distribution*

Occurs in pools or damp sheltered areas through much of the littoral, extending to the sublittoral; epiphytic, commonly on *Fucus, Saccorhiza, Laminaria* and larger Rhodophyta.

BRITISH ISLES: Channel Islands, Cornwall, Devon, Dorset, Isle of Wight, Sussex, Kent, Norfolk, Yorkshire, Cheshire, Isle of Man; Caernarvonshire, Angelsey; Ayr, Bute, Argyll, Orkney, Aberdeen; Dublin, Cork, Galway, Mayo, Down.

WORLD: Eastern Atlantic from western Norway to Canaries and Morocco; western Mediterranean; western Atlantic from southern Massachusetts to Florida; Texas, West Indies; reported for New Zealand and Tasmania.

Observations

Callithamnion byssoides has been confused with *C. corymbosum* and *C. roseum*, but the species has a consistent ecological and geographical distribution. Critical cases are few in the British Isles, but this is not necessarily true for the western part of the north Atlantic. *C. byssoides* and *C. corymbosum* are occasionally confusable where the former lacks bisporangia. *C. byssoides* usually lacks the apical pseudodichotomy at unlimited functional apices, the pseudodichotomies at peripheral lateral apices, and the hyaline hairs typical of *C. corymbosum. C. corymbosum* has much coarser growth and all cells are multinucleate. *C. byssoides* is finer than *C. roseum,* another multinucleate species. Mature cells near the functional apices of *C. byssoides* are less than 20 μm maximum breadth, whereas in *C. roseum* they exceed 30 μm. The often greater length of cells of *C. byssoides* emphasizes this distinction.

The sequence of morphological phases in the life history has been established for material identified as *Callithamnion byssoides* from Port Aransas, Texas (Edwards, 1969) and from Wrightsville Beach, North Carolina (Kapraun, 1978). These materials may not be conspecific with British *C. byssoides*, a point already correctly made by Rueness & Rueness (1980). Chromosome counts of $n = 28–33$ were reported in thalli from an undefined location in the British Isles (Harris, 1962). The recent study (Rueness & Rueness, 1980) on Norwegian material of *C. byssoides* established both a *Polysiphonia*-type life-history for the

*For this and all subsequent species, distribution is stated on the basis of the old county boundaries. The newly-formed counties are both too large in area (particularly in Wales and Scotland) for effective discussion, and not yet well enough comprehended in geographical terms.

European taxon and an interesting mode of perennation. It is curious that although the alga is normally epiphytic (so reported by most authors, including this study), the perennating creeping filaments that subsequently gave rise to *C. byssoides* plants were borne on the ascidian *Ciona intestinalis*. Further field studies of this phenomenon elsewhere are required.

2. Callithamnion corymbosum (Smith) Lyngbye, *Tent. Hydr. Dan.* : 125 (1819).

Conferva corymbosa Smith in Smith & Sowerby, *Engl. Bot.*: pl. 2352 (1811).
Ceramium versicolor C. Agardh, *Syst. Alg.*: 140 (1824).

Thallus pinkish-red, or brownish to deep red in colour; to 55 mm in height; bushy, flaccid, usually with a single recognizable main axis; branching commonly pseudodichotomous throughout, but with all gradations from monopodial to complete pseudodichotomy; principal laterals of unlimited growth irregular in position and number; growth form irregular to more or less regular; main axes 40–270 (–300) μm in breadth; commonly corticate but sometimes ecorticate; occasional adventitious branching from the corticating filaments, but lacking formation of adventitious matrix; axial cells in straight lines, some curvature but no zigzags; branching often straggly and inconsistent in older parts towards base, younger branches show spiral pseudodichotomous arrangement, divergence angles usually about 30°, rarely more; peripheral laterals borne toward apices on axes of various orders, simple and spiral, or pseudodichotomous; apical development pseudodichotomous in peripheral laterals axes; apical cells of axes surpassed by peripheral laterals; apical cells of peripheral laterals 5–10 μm in diameter, axial apical cells often smaller; hairs apical or subapical, often present on all apical cells but equally often absent; cells at base of thallus 170–250 μm in breadth, 25–35 μm in mature cells near apices; length-to-breadth ratios of cells 6–12 to 1; cells multinucleate, except for a few cells near apices.

Gametangial thalli dioecious. Spermatangiophores multi-branched, one to two cells in length, often several on each cell of peripheral or high order laterals; 2 to 4 spermatangia on ultimate cells of spermatangiophores; spermatangia 5–8 μm.

Procarps normally formed just behind apices of principal axes and branches; usually 2 support cells, occasionally only one; carpogonial branch usually in form $\begin{matrix} & & 4 \\ & & \uparrow \\ 1 \rightarrow & 2 \rightarrow & 3, \end{matrix}$ less often completely straight; two one-celled gonimoblasts from each central cell, commonly two gonimolobes on primary gonimoblast, only one on secondary gonimoblast, but one or more gonimolobes occasionally missing; gonimolobes rounded, usually finally lacking subsidiary lobing; carposporangia 25–35 μm in diameter.

Tetrasporangia globose, 45–60 × 55–65 μm, sessile, one or more on each cell of peripheral laterals; often appearing to be axillary to pseudodichotomies.

The growth form of *Callithamnion corymbosum* can be very variable. Thalli may possess either distinct axes bearing spirally arranged branches and simple peripheral laterals or with branches and peripheral laterals developing at same rate as principal axes, producing a pseudodichotomous aspect. Pseudodichotomies may occur throughout a plant, but are most common only in the upper parts. The number of hairs is variable; some thalli have hairs on almost all apical cells, others a few scattered hairs, some totally devoid of them. Harris (1959) noted in Galway that plants of greater shelter had a few spirally-arranged hairs in the upper parts while thalli of greater exposure showed pseudodichotomies and hairs on nearly all apical cells. This is not a difference that is consistent in such conditions (see Price, 1978).

Thalli with gametangia reported between April and November; tetrasporangia occur throughout the year.

Ecology and distribution

Usually epiphytic, on *Codium fragile, Fucus vesiculosus,* or *Zostera*; occasionally epilithic in lower littoral, usually in standing water, pools and channels; known in the sublittoral to at least 22 m in sheltered bays.

BRITISH ISLES: Channel Islands, Cornwall, Devon, Dorset, Hampshire, Isle of Wight, Sussex, Somerset, Cheshire, Isle of Man, Suffolk, Northumberland; Pembroke, Cardigan, Merioneth, Caernarvonshire, Anglesey; Ayr, Bute, Argyll, Ross & Cromarty, Orkney, Aberdeen, Fife, Midlothian; Dublin, Wexford, Cork, Galway, Mayo, Down.

WORLD: Eastern Atlantic, Norway (Nordland) to Canaries; western Baltic, Mediterranean and Black Sea; Western Atlantic, Newfoundland to New Jersey; West Indies; Australia; Japan.

Observations

Callithamnion corymbosum has been confused with *C. byssoides* and *C. roseum*. Pseudodichotomies at apices are absent in *C. roseum* and the hairs characteristic of *C. corymbosum* are also lacking in that species. These features are also absent in *C. byssoides* but *C. corymbosum* has much coarser growth and multinucleate cells.

The sequence of phases in the life history of *Callithamnion corymbosum* was established in culture for material from Helgoland (Hassinger-Huizinga, 1952). In the present study, a few plants have been observed with both tetrasporangia and carposporophytes and some with tetrasporangia and alleged bisporangia. Hassinger-Huizinga reported the occurrence in Helgoland material of thalli with tetrasporangia and either spermatangia or procarps in her cultural studies. She claimed that the expression of gametangia and tetrasporangia is governed by the addition or deletion of a chromosome. These data must be regarded with caution since neither figures nor photographs of the chromosome complements are given and the results necessitate absolute accuracy in counting chromosomes with a complement of about 60 in a nucleus 5 µm in diameter.

In Newfoundland, *Callithamnion corymbosum* occurs as tetrasporangial thalli which appear to reproduce only by fragmentation (Whittick, 1978).

Chromosome counts in *Callithamnion corymbosum* have been reported in material from various locations as follows: Helgoland: = 30–32; 2n = 60–64 (Hassinger-Huizinga, 1952), British Isles: n = 27–29 (Harris, 1959), British Isles: n = 28–33 (Harrris, 1962), British Isles: n = c. 28 (Harris, 1966), Newfoundland: 2n = 57–65 (Whittick, 1973).

3. Callithamnion decompositum J. Agardh, *Sp. Gen. Ord. Alg.* 2 (1) : 45 (1851).

Thallus light red in colour; somewhat rounded pyramidal in outline (see Price, 1978: 283, fig. 15*b*); rarely attaining more than 20 mm in length; main axis little corticate in British specimens, although dense cortication reported elsewhere; branching usually strictly distichous, commonly commencing at the second cell of major axes, branches restricted to the adaxial side of the lower two cells of primary laterals giving a slightly secund appearance in a few specimens; peripheral laterals attenuate and much ramified, causing flabellate spreading distal effect that rounds off the pyramidal outline; hyaline hair points to 60 µm in length reported in southern collections, but not noted in northern British material; cells of main axes relatively large, 130–550 µm in length,70–200 µm in breadth in mature material; chloroplasts said to be polygonal-discoid when young, becoming elongate in older cells (in British material the variation between variable discoid and elongate does not appear to be correlated with age); masses of proteinaceous material present.

Gametangial thalli unknown for the British Isles; in non-British material dioecious; spermatangiophores 2–4 celled, occurring on the first or second cells of laterals, each cell of the spermatangiophore bearing 3 or 4 spermatangia; spermatangia *c.* 5 × 8 µm.

Procarps formed behind apices of lateral axes, commonly with two support cells; carpogonial branch 'U'-shaped, trichogyne to 95µm in length; gonimolobes cordate, 41–70 × 35–47 µm; carposporangia 10 × 12 µm in diameter.

Tetrasporangia uncommon in British material; rounded or ovoid, to 55 × 65 µm in diameter, usually sessile, occasionally pedicellate, occurring adaxially on peripheral laterals; spore arrangement usually tetrahedral, occasionally irregular.

Parasporangia the most usual reproductive structure formed in British material, lobed or irregular, sometimes linear, depending on state of development, 22–56 × 11–22 μm, usually at the apices of adaxial products of peripheral lateral cells; individual paraspores 9–18 μm.

The form range of *Callithamnion decompositum* is not fully elucidated, either in the British Isles or elsewhere (Price, in preparation). This is partly due to uncertainties regarding the status of material referred by other workers to *C. bipinnatum, C. tripinnatum, C. gallicum* or *C. caudatum.* For a recent study of *C. bipinnatum,* see Rueness & Rueness (1980).

Ecology and distribution

Epiphytic on other algae, but also epizoic and epilithic; usually sublittoral, to 30 m, but also reported elsewhere in the lower littoral. Usually rather few thalli present.

British Isles: Known only for Argyll (Mull), Inverness (Rhum) and Zetland, but probably occurs more widely.

World: Eastern Atlantic from the Faeroes to Sénégal. The species may also occur in Denmark and Norway, for which areas the relationships with material referred to *Callithamnion bipinnatum* require elucidation. Recent work on the latter species by Rueness & Rueness (1980) suggests that, whatever the application by some authors of that name, there is a good taxon concealed amongst the doubtful applications.

Observations

Callithamnion decompositum may be confused with *C. hookeri* in the lower littoral and shallow sublittoral, where both species have similar appearance and dimensions. The apical organization of the two species is, however, usually quite distinct with virtually absolute distichy in *C. decompositum* and some spiral arrangement of the ultimate laterals somewhere on the plant in *C. hookeri.* Below the shallow sublittoral, *C. hookeri* becomes more lax and less branched, whereas *C. decompositum* retains its characteristic growth-form.

Although parasporangia are the most reproductive structures found in British material, there is insufficient information to comment on their phenology.

Nothing is known of the life history of *Callithamnion decompositum.* These northern populations are parasporangial, although gametangia and/or tetrasporangia are produced by material from areas south of the British Isles. In Finistère, parasporangia have been reported mixed with tetrasporangia. Data on the life history in northern material will, it is hoped, be more fully available when the Faeroe Islands specimens at present in culture at the University of Oslo (J. and M. Rueness) have developed beyond vegetative growth from the originally-released tetrasporangia.

4. Callithamnion granulatum (Ducluzeau) C. Agardh, *Sp. Alg.* **2** (1) : 177 (1828).

Ceramium granulatum Ducluzeau, *Essai Hist. Nat. Conf. Montpellier*: 72 (1806).
Callithamnion harveyanum J. Agardh in *Linnaea* **15** : 45 (1841).
Callithamnion grande J. Agardh, *Alg. Mar. Med. Adr.*: 73 (1842).

Thallus pale straw, brownish, rust, to purple-red or dark red in colour; to 150 mm in height; robust but highly flexible, flaccid in water; spongy in texture and appearance, but less so than in *C. sepositum*; appearing as regular or irregular, simple or compound pine-tree like pyramids; main axes rarely bifurcate near base, to 3 mm or more in breadth, but probably greater in larger specimens; strongly corticate throughout; cortication develops dense matrix of short tightly-woven adventitious laterals, giving rise occasionally to peripheral laterals of normal form; main axial cells almost invisible without dissection; axial cells in straight lines, length-to-breadth ratios of any visible upper axial cells usually 1·5 to 3 : 1; branching monopodial, associated with pseudo-dichotomy at all levels and especially obvious at

peripheries of thallus; divergence angles greater than 45°, sometimes 90°, unless strongly appressed in corymbose clusters; apical cells of indeterminate laterals buried in the corymbose clusters of peripheral laterals, normally needing dissection for examination; peripheral laterals often spreading, but also frequently grouped in corymbose clusters, that represent individual lateral systems, to 700 µm in breadth (Price, 1978 : Fig. 11A–C); individual peripheral laterals often straight although occasionally curved in the corymbose clusters; greatest width of peripheral lateral at or near base; cells (1–) 2–4 (–6) per peripheral lateral, usually more or less rectangular, with some apical narrowing; peripheral lateral apical cell a short cylinder to roundly-truncated cone, 17·6 ± 6·6 µm in length; with occasional terminal or subterminal hyaline hairs.

Gametangial thalli dioecious or (less often) monoecious. Spermatangial groups hemispherical, rarely coalescent; spermatangiophores multibranched, branches 3–5 cells long; two to four spermatangia on peripheral cell of each branch; spermatangia ovate to ellipsoid, 6 × 8 µm.

Procarps formed just behind functional apices of penultimate and lower order laterals; usually two support cells, but occasionally one; carpogonial branch form difficult to interpret, but straight, with minor variations, and zigzag (the more usual) noted; carpogonial maximum breadth 18 µm; trichogyne to 70–240 µm in length; gonimoblasts single-celled, two from each central cell; usually one gonimoblast giving rise to one gonimolobe, occasionally gonimolobes missing; gonimolobes rounded without subsidiary lobing: carposporangia 25–35 µm in diameter.

Tetrasporangia initially apical on cell below peripheral dichotomies, spreading to cells of peripheral laterals, large, globose to ellipsoid, 45–60 × 50–60 µm, never more than one per bearing cell; polysporangia reported but never observed in the present study.

Detailed consideration of some aspects of growth form variation in *Callithamnion granulatum* is given in Price (1978).

Reproductive phenology in *Callithamnion granulatum* is variable with location, year and individual thalli, although patterns can be perceived. Detailed information is being published elsewhere.

Ecology and distribution

Occurs in rock pools and on emersed damp surfaces in the lower littoral of wave-exposed shores; commonly epiphytic, very rarely epilithic, frequently epizoic on *Mytilus, Patella* and *Balanus,* especially in blanket populations; reported from the sublittoral, but all such reports erroneous except in very shallow conditions (to 0·5 m).

British Isles: Channel Islands, Cornwall, Devon, Dorset, Isle of Wight, Yorkshire, Isle of Man; Pembroke, Caernarvonshire, Anglesey; Ayr, Bute, Argyll, Inverness, Ross & Cromarty, Orkney, Zetland, Angus, Fife, Midlothian, East Lothian; Antrim, Mayo, Galway, Clare, Cork, Wexford, Wicklow, Dublin, Down.

World: North-eastern Atlantic from Shetlands to Morocco, perhaps to the Gulf of Guinea, locally (Liberia, Côte d'Ivoire, Ghana); Mediterranean. Material reported from the Faeroes all appears referable to the exposed-water form of *Callithamnion hookeri*, growing epiphytically on *C. sepositum*.

Observations

The only possible confusions are with *Callithamnion sepositum* or *C. spongiosum*. The principal criterion for discrimination is the most usual number of cells in the highest order peripheral laterals, with 1 or 2 cells in *C. spongiosum*, 3 to 4 in *C. granulatum* and 7 to 9 in *C. sepositum*. *C. granulatum* may also be distinguished from *C. sepositum* in its consistent pseudodichotomy and the basal, or near basal, maximum width of the peripheral laterals. The greatest difficulty is in discriminating from *C. spongiosum,* with which it tends to occur in mixed populations although intermediate forms are lacking. Cotton (1912) distinguished

between the two species, although the ecological differences which he noted do not hold consistently.

Little published information is available on the life history of *Callithamnion granulatum*; all exposed shore forms are difficult to culture. Harris (1962) reported a chromosome number of n = 28–33 in material identified by him as *C. purpurascens* and possibly referable to this entity.

5. Callithamnion hookeri (Dillwyn) S. F. Gray, *Nat. Arr. Br. Pl.* **1** : 324 (1821).

Conferva hookeri Dillwyn, *Br. Conf.*: pl. 106 (1809).
Callithamnion roseum β tenue Lyngbye, *Tent. Hydr. Dan.*: 126 (1819).
Ceramium scopulorum C. Agardh, *Syst. Alg.*: 132 (1824).
Callithamnion scopulorum C. Agardh, *Sp. Alg.* **2** (1) : 166 (1828).
Callithamnion polyspermum C. Agardh, *Sp. Alg.* **2** (1) : 169 (1828).
Callithamnion brodiaei Harvey in Hooker, *Eng. Fl. Sir J. E. Smith* **5** : 340 (1833).
Callithamnion grevillei Harvey in Hooker, *Eng. Fl. Sir J. E. Smith* **5** : 345 (1833).
Callithamnion spinosum Harvey in Hooker, *Eng. Fl. Sir J. E. Smith* **5** : 345 (1833).
Callithamnion acrospermum J. Agardh, *Sp. Gen. Ord. Alg.* **2** (1) : 52 (1851).

Thallus of widely different colours but usually dark to brownish red; to 70 mm or more in height; bushy, straggly, or sparsely branched, sometimes even reduced to a single main axis; main axis or axes 300–500 µm in breadth, commonly corticate, often with reduced cortication, or even none in younger material; cortication often producing adventitious laterals, when extreme forming a matrix that may be over 2 mm overall breadth; branching very variable, from regular alternate-spiral to highly irregular; peripheral laterals distichous or spiral, but not usually overtopping the apex of main axis, borne on penultimate laterals with strong axial zigzag; apical cells rounded, basal breadth 5–10 µm; cell numbers and dimensions in peripheral laterals highly variable; cells of peripheral laterals cylindrical or slightly tapered; mature cells near base of thallus 50 to 100 µm maximum diameter, reducing to 40 to 80 µm near apex, length-to-breadth ratios varying between 0·5 to 1 and 5 to 1.

Gametangial thalli dioecious. Spermatangiophores one, rarely more, per cell of peripheral laterals, variable in form even in same thallus; most spermatangiophores consisting of a single cell with a single secund branchlet, 3 to 4 cells in length, others with a series of secund branchlets; ultimate cells of branchlets bearing 2 to 4 spermatangia, usually secund but sometimes distichous; spermatangia 4 × 8 µm.

Procarps formed just behind apices of axes and indeterminate laterals; carpogonial branch of variable form, from straight to zigzag; usually developing two auxiliary cells after fertilization, but occasionally only one; each auxiliary cell producing two single-celled gonimoblasts, with one or two gonimolobes, although the second-developed filament may produce only one or even none; gonimolobes lobed or simple, usually rounded, but sometimes pointed or even conical; carposporangia at maturity 35–50 µm in diameter.

Tetrasporangia globose or nearly so, sessile, 40–60 × 45–60 µm, borne adaxially on peripheral laterals, usually one per cell, but occasionally with a second tetrasporangium borne abaxially. Bisporangia occur rarely, mixed with tetrasporangia, and may represent only an aberrant or developmental stage of the latter. Parasporangia replacing vegetative lateral filaments reported widely, but not authenticated in the British Isles. Monosporangia reported, but probably nothing more than tetrasporangial initials.

The overall thallus form is highly variable under different environmental conditions and in different locations. So far as can be determined, there are no consistent morphological distinctions between *Callithamnion hookeri* and the entities usually treated under the names *C. scopulorum, C. brodiaei* and *C. polyspermum.* The thalli which have been referred to *C. scopulorum* occur in the upper littoral in damp locations as clumps or local turfs. The customary epiphytic littoral populations tend to be lax whereas in situations exposed to wave-action the thalli are robust, short, stubby and much branched. The sublittoral

populations tend to be extremely lax. Analysis of this variation in respect to previous nomenclature and taxonomy is given in Price (1978).

Reproductive phenology in *Callithamnion hookeri* is variable with location, year and individual thalli, although patterns can be perceived. Detailed information is being published elsewhere.

Ecology and distribution

Occurs in rock pools and on emersed damp surfaces in the lower littoral of wave-exposed shores; commonly epiphytic, rather rarely epilithic, frequently epizoic on *Mytilus, Patella* and *Balanus*.

British Isles: *Callithamnion hookeri* is probably present throughout the British Isles, occurring under appropriate circumstances. Positive identifications are, however, available only for the following counties; Channel Islands, Cornwall, Devon, Dorset, Hampshire, Sussex, Kent, Essex, Suffolk, Norfolk, Lincolnshire, Yorkshire, Durham, Northumberland, Somerset, Cheshire, Cumberland, Isle of Man; Glamorgan, Pembroke, Cardigan, Caernarvonshire, Anglesey; Dumbarton, Wigtown, Ayr, Bute, Renfrew, Argyll, Inverness, Ross & Cromarty, Orkney, Zetland, Sutherland, Moray, Aberdeen, Kincardine, Angus, Fife, Midlothian, East Lothian, Berwick; Antrim, Londonderry, Donegal, Leitrim, Mayo, Galway, Clare, Limerick, Kerry, Cork, Waterford, Wexford, Wicklow, Dublin, Down.

World: *Callithamnion hookeri* is extremely widespread but a precise statement of its total distribution is difficult in view of its great variability and the need to clarify the status of material referred to such entities as *C. bipinnatum, C. tripinnatum, C. pusillum, C. hirtellum, C. truncatum,* etc. The species occurs in the north Atlantic in Iceland and between northern Norway and the Canary Islands and Morocco, occurring also (Price, in press) in areas of cold upwelling in the Gulf of Guinea (and perhaps sparsely in Angola), on the Baltic Sea coast of Germany, and from Newfoundland (South & Hooper, 1980) southward. The reported occurrence of various entities possibly referable to this species in the Mediterranean must await taxonomic clarification; the same comment applies to reports from the Pacific Ocean.

Observations

The life history of *Callithamnion hookeri* has been shown by culture studies of British material to consist of a sequence of gametangial, carposporangial and tetrasporangial phases (Edwards, 1979), although nothing is known of the chromosome counts. In populations from the west coast of Sweden, it has been shown that paraspores develop into parasporangium-bearing thalli for several successive generations (Rueness & Rueness, 1978). The role of the alleged monosporangia has not been established. On the relations between life-history, tolerance levels, and distribution pattern, see van den Hoek (in press).

6. Callithamnion roseum (Roth) Lyngbye, *Tent. Hydr. Dan.*: 126, tab. 39 (1819).

Ceramium roseum Roth, *Archiv Bot. (Römer)* **1** (3): 47 (1798).
Conferva rosea (Roth) Smith in Smith & Sowerby, *Engl. Bot.*: pl. 966 (1802).
Callithamnion octosporum C. Agardh, *Sp. Alg.* **2**(1): 177 (1828).

Thallus pinkish to purple-red; to 80 or more mm in height; bushy and fairly robust, less delicate or flouncy than *Callithamnion byssoides* or *C. corymbosum,* but still flaccid; usually with one main axis; main axis to 1·0 mm in breadth, sometimes ecorticate but commonly with at least a few cortical filaments from lower branches, occasionally moderately corticate but no development of adventitious matrix from cortication; branching monopodial but sometimes with pseudodichotomous aspect below carposporophyte; axial (indeterminate) branches irregular in position and number, variable in length, especially at base of plant, spirally arranged in upper parts; peripheral laterals usually simple, upsweeping and incurving, spiral; apical cells of peripheral laterals 5–10 μm in breadth; apical cells of main axis and main branches surpassed by subordinate peripheral laterals; cells at bases of plants 130–225 μm in breadth; tapering; mature cells, near apices, 30–35 μm in breadth; length-to-breadth ratio 5–12 to 1 but cells usually shorter, more robust, than *C. byssoides*; cells usually

multinucleate except immediately behind apices; chloroplasts irregularly discoid in young cells, forming continuous ribbons with age.

Gametangial thalli dioecious. Spermatangiophores two cells in length, multibranched, often several on each cell of peripheral laterals; two to four spermatangia on ultimate cells of spermatangiophore cluster; spermatangia 5 × 8 μm.

Procarps formed behind apices of main axes and branches, commonly with two support cells, rarely only one; carpogonial branch straight, occasionally zigzag; two gonimolobes from each central cell, each one-celled; commonly two gonimolobes on first gonimoblast, but only one on secondary gonimoblast; one or more gonimolobes occasionally missing; gonimolobes usually lacking subsidiary lobing, rounded; carposporangia 20–35 μm in diameter.

Tetrasporangia globose, 40–50 × 45–55 μm, sessile, often abundant, one or more, usually adaxial, on each mature cell of peripheral laterals.

Spermatangial thalli of *Callithamnion roseum* tend to be more delicate than tetrasporangial or sterile specimens, but the degree of robustness varies enormously.

Fertile thalli appear to occur at all times of the year, but there is considerable variation in the reproductive organs present according to individual thallus, year, time and location.

Ecology and distribution

Epiphytic on other algae in lower littoral in sheltered conditions or sheltered niches on more wave-exposed shores; can extend into the sublittoral to at least 20 m. A characteristic habitat is just below water level on floating structures in areas of somewhat fluctuating salinity.

British Isles: Channel Islands, Cornwall, Devon, Hampshire, Sussex, Kent, Suffolk, Norfolk, Lincolnshire, Isle of Man; Caernarvonshire, Anglesey; Cork, Galway, Wexford, Dublin. Probably widespread.

World: Eastern Atlantic from Norway to Portugal; Baltic; eastern coast of the United States.

Observations

Callithamnion roseum may be confused with *C. corymbosum* and *C. byssoides,* but lacks pseudodichotomous apical development and the hairs which occur quite commonly in British *C. corymbosum. C. roseum* has coarser growth than *C. byssoides,* with multinucleate cells.

Tetrasporangia occur in all months of year in most areas of the British Isles. Gametangial plants and carposporophytes detected April–November. Little published information exists on the life history of *Callithamnion roseum.* Bisporangia or carposporophytes have been reported on a few tetrasporangial plants. Chromosome number reported, doubtfully, as n = *c.* 39 (Harris, 1962, 1966), but no other data available.

7. **Callithamnion sepositum** (Gunnerus) P. Dixon & J. Price, *comb. nov.*

Conferva seposita Gunnerus, *Fl. Norv.*: 116 (1772).
Conferva purpurascens Hudson, *Fl. Angl.,* 2nd ed. **2** : 600 (1778).
Conferva arbuscula Dillwyn, *Br. Conf.*: pl. 85 (1807).
Ellisius glaber S. F. Gray, *Nat. Arr. Br. Pl.* **1** : 333 (1821).
Phlebothamnion faroense Kützing, *Tab. Phyc.* **14** : 30 (1864).
Phlebothamnion scoticum Kützing, *Tab. Phyc.* **14** : 30 (1864).

Thallus dark red to dark purple in colour, distally bleaching to straw-coloured; robust and spongy but highly flexible, the texture resembling wet wool; main axes and laterals strongly corticate, covered throughout by a matrix of short, adventitious laterals obscuring the axes; axes from 310 μm to more than 5 mm in breadth; branching alternate-pinnate throughout, with occasional apparent aberrant pseudodichotomies; intermediate laterals arising in all directions; peripheral laterals grouped into tightly-packed, incurved, corymbose clusters,

700 to 1400 μm in breadth (Price, 1978 : Fig. 10A–C); apical cells truncated cones, length frequently greater than breadth, length 20·5 ± 5·0 μm, basal breadth 16·60 ± 4·2 μm, apical breadth 5·50 ± 2·5 μm; cell numbers in peripheral laterals (2–) 7–9 (–16); peripheral laterals 125–539 μm in length × 24–60 μm in breadth, position of the maximum breadth usually well above the base or lower half parallel-sided; cells of peripheral laterals cylindrical, the maximum breadth equal to the length.

Gametangial thalli monecious or dioecious, predominance apparently varying with region. Spermatangial thalli with dense spermatangia within the apical corymbose clusters, sometimes in localized areas, sometimes widespread throughout; initial stages adaxial along incurved peripheral laterals, but subsequently spreading to form coalescent cushions along the lengths of whole laterals.

Carpogonial thalli usually bearing abundant procarps; position of procarps variable, above or below outer forkings on peripheral laterals in heavy-cropped specimens; two support cells developed, frequently only one visible; carpogonial branch apparently U-shaped but sometimes with possible zigzag; carpogonia 15–26 μm in breadth, trichogyne to 240 μm in length, always twisted, occasionally with swellings or bifurcations; carposporophytes large and conspicuous when fully grown, normally paired on opposing support cells, occasionally unilateral; in luxuriant growth, carposporangia becoming angular through lateral pressure; rounded-off carposporangia 70 × 70 μm.

Tetrasporangia sub-spherical to spherical, sessile; (42–) 59–77 (–110) × (37–) 55–70 (–100) μm; adaxial, occasionally abaxial on cells of outer peripheral laterals.

There are correlations between the form of mature plants and reproductive state. Tetrasporangial specimens show luxuriant clumped and bushy branching, while carposporangial thalli show sparser, more open, branching with longer laterals, which however do not contain more cells. Spermatangial specimens are intermediate between these two. Hyaline hair points can occur on any material but particularly on carpogonial plants. During winter and early spring, thalli of *Callithamnion sepositum* are very straggly and tend to lack the peripheral corymbose clusters of laterals.

Reproductive phenology in *Callithamnion sepositum* is variable with location, year and individual thalli, but patterns can be perceived. Detailed information is being published elsewhere.

Ecology and distribution

Commonly epilithic on steep slopes or epizoic on shells of *Patella, Balanus* and *Mytilus*; in blanket populations, occasionally epiphytic on *Corallina* or on the bases of exposed *Fucus vesiculosus*; very rarely in pools except in blanket populations.

British Isles: Cornwall, Devon, Yorkshire, Durham, Northumberland, Isle of Man; Pembroke, Caernarvonshire, Anglesey; Wigton, Ayr, Bute, Argyll, Inverness, Ross & Cromarty, Sutherland, Caithness, Orkney, Zetland, Banff, Aberdeen, Angus, Fife, Midlothian, East Lothian, Berwick; Waterford, Cork, Kerry, Clare, Galway, Mayo, Donegal.

World: Norway, Faeroes, and Iceland.

Observations

Callithamnion sepositum is similar in size, appearance and growth in blanket populations on the shore to *C. granulatum*, but mature thalli of *C. sepositum* lack the symmetrical appearance of those of *C. granulatum*. See pp. 121–2; 126–7 where the differences are discussed in detail.

Little published information is available on the life history of *Callithamnion sepositum*; all exposed shore forms are difficult to culture. Harris (1962) reported a chromosome number of n = 28–33 in *C. purpurascens,* possibly referable to this entity.

8. Callithamnion spongiosum Harvey in Hooker, *Engl. Fl. Sir J. E. Smith* **5** : 346 (1833).

Thallus through pale straw or brownish or rust, to purple-red or dark red in colour according to season and environment; to 50 mm in height; robust but highly flexible, flaccid in water; spongy in texture and appearance, but (like *Callithamnion granulatum*) less so than in *C. sepositum*; appearing as regular or irregular, simple or compound pine-tree like pyramids; main axes rarely bifurcate near base; to 3·0 mm in breadth, but probably greater in larger specimens; strongly corticate throughout; cortication developing dense matrix of short tightly woven adventitious laterals, giving rise occasionally to peripheral laterals of normal form; main axial cells almost invisible without dissection; axial cells in straight lines, length-to-breadth ratios of any visible upper axial cells usually 1·5 –3 to 1; branching monopodial, associated with pseudodichotomy at all levels but especially obvious at periphery of thallus; divergence angles greater than 45°, sometimes 90°; indeterminate apical cells buried in corymbose clusters (representing individual lateral systems) of peripheral laterals, normally needing dissection for examination; peripheral laterals often spreading, frequently grouped in corymbose clusters to 700 μm in breadth; individual peripheral laterals usually straight (although occasionally curved in corymbose clusters) consisting of one, less often two, cells, greatest width at or near base; cells usually more or less cylindrical, with some apical narrowing; apical cell short cylinder or rounded, 17·6 ± 6·6 μm in length; occasional terminal or subterminal hyaline hairs.

Gametangial thalli dioecious or monoecious. Spermatangial cluster hemispherical, rarely coalescent; spermatangiophores multibranched, branches 3–5 cells long; two to four spermatangia on peripheral cell of each branch; spermatangia ovate to ellipsoid, 6 × 8 μm.

Procarps formed just behind functional apices of penultimate and lower order laterals; usually two support cells, but occasionally one; carpogonial branch form difficult to interpret, but straight (with minor variations) and zigzag noted; carpogonial maximum breadth 18 μm, trichogyne to 70–240 μm in length; gonimoblasts single-celled, two from each central cell; usually one gonimoblast giving rise to one gonimolobe, but occasionally gonimolobes missing, mature gonimolobes rounded without subsidiary lobing; carposporangia 25–35 μm in diameter.

Tetrasporangia initially apical on cell below peripheral dichotomies, spreading to cells of peripheral laterals, large globose to ellipsoid, 45–60 × 50–60 μm, never more than one per bearing cell; polysporangia reported but never observed in the present study.

So far as can be determined from the sparse material available, the growth form variation in *Callithamnion spongiosum* is similar to that of *C. granulatum*, discussed on p. 120 et seq.

Callithamnion spongiosum occurs too sparsely for any meaningful comments to be made on the reproductive phenology of this species.

Ecology and distribution

Occurs in rock pools and on emersed damp surfaces in the lower littoral, commonly epiphytic, less frequently epizoic on *Mytilus, Patella* and *Balanus*. Very rarely in large populations; usually mixed as sporadic thalli with *Callithamnion granulatum*.

British Isles: Cornwall, Devon, Isle of Man; Pembroke, Caernarvonshire, Anglesey; Ayr, Bute; Antrim, Dublin.

Other records (Sussex, Yorkshire, Fife, Zetland, Angus, Channel Islands) have proved on re-examination to be erroneous, although there is no reason to doubt the sporadic occurrence of the entity in western areas.

World: No verifiable records are known, but on the basis of present knowledge the presence of this species in the least north-west France is probable.

Observations

The only possible confusions are with *Callithamnion sepositum* or *C. granulatum*. The most usual number of cells in the higher order peripheral laterals is the prime characteristic for

discrimination, with 1 or 2 cells in *C. spongiosum*, 3 to 4 in *C. granulatum* and 7 to 9 in *C. sepositum*. *C. spongiosum* may also be distinguished from *C. sepositum* in its consistent pseudodichotomy and the basal maximum width of the peripheral laterals. The greatest difficulty is in discriminating from *C. granulatum,* with which it tends to occur in mixed populations, although intermediate forms are lacking. Cotton (1912) distinguished between the two species, although the ecological differences which he noted do not consistently hold.

It may be that the rarity of occurrence of specimens amongst *Callithamnion granulatum* populations represents the detected manifestation of tendencies towards speciation in a genome currently still interfertile with the *C. granulatum* from which it arises. If this is so, the expected intermediates must be being dismissed as plants of *C. granulatum*. The inconsistency and sparseness of appearance in particular *C. granulatum* populations may indicate a present lack of success in establishment as a separate and defined breeding population (eventually, species). It will be interesting to see if specimens of *C. spongiosum* become more frequent in the field in the (imponderable) future, with some gradual emphasis of ecological tolerance differences, at present not recognizable to us.

No published information is available on the life history of *Callithamnion spongiosum*; all exposed shore forms are difficult to culture. Harris (1962) reported a chromosome number of n = 28–33 in material referred by him to *C. purpurascens*, possibly referable to this entity.

9. Callithamnion tetragonum (Withering) S. F. Gray, *Nat. Arr. Br. Pl.* **1** : 329 (1821).

Conferva tetragona Withering, *Arr. Br. Pl.,* 3rd ed. **4** : 405 (1796).
Ceramium fruticulosum Roth, *Cat. Bot.* **2** : 183 (1800).
Conferva fruticulosa Wulfen, *Crypt. Aquat.* : 26 (1803).
Ceramium brachiatum Bonnemaison in *Mém. Mus. Hist. nat. Paris* **16** : 136 (1828).
Ceramium dudresnayi Bonnemaison in *Mém. Mus. Hist. nat. Paris* **16** : 125 (1828).
Ceramium guttatum Bonnemaison in *Mém. Mus. Hist. nat. Paris* **16** : 127 (1828).
Callithamnion fruticulosum J. Agardh in *Linnaea* **15** : 46 (1841).

Thallus red, brownish-red to rust in colour; robust, coarser than all other species except *Callithamnion tetricum*, irregularly pyramidal in outline, to 110 mm in height; usually a single main axis in a thallus, apparent basal division into several principal axes often resulting from separate development of adjacent spores; branching regularly spiral, occasionally irregular towards base of main axis, larger laterals similar to main axis; main axis strongly corticate, 233 to 550 μm (to 1 mm) in breadth; adventitious branching from the cortication absent or sparse; axial cells in linear rows, rarely even distal axial zigzag; length-to-breadth ratios of axial cells easily seen through cortication, usually less than 3 to 1; cell breadth tapering from axial base to apex, from 200–300 to 90–110 μm; apices surpassed by clustered peripheral laterals, latter without the corymbose grouping that occurs in many other exposed shore species; older lower order laterals easily confused with main axes when detached; peripheral laterals incurved, often strongly so giving 'awl'-shape, occasionally straighter, longer and narrower, appearing almost parallel-sided ('*brachiatum*'); cells of peripheral laterals barrel-shaped ('*tetragonum*') or cylindrical ('*brachiatum*'); apical cells of peripheral laterals small in relation to products, more or less conical, with pointed apices, 12 ± 3 μm, in length, 10 ± 4 μm in breadth at base; cells below determinate lateral apices truncated cones; breadth of immediate derivatives equal to or greater than length; cells usually two or more times as long as apical cell; cells in peripheral laterals 150 to 700 μm in length, maximum breadth, basal to median in position, (11–) 40–165 μm; hairs absent from British material; cells multinucleate, except near apices; chloroplasts irregularly discoid, occasionally becoming long thin ribbons or irregular masses.

Gametangial thalli usually monoecious, habitually so in some populations. Spermatangiophores many-branched, branches 3 to 5 cells long, forming unilateral adaxial tufts, 60 ± 6μm in length, 30 ± 7 μm in height, one per cell of peripheral laterals, borne near apical septum, rarely coalescent; ultimate cells bearing two to four spermatangia per cell; spermatangia 5 × 8 μm.

Procarps formed behind indeterminate apices of peripheral branch systems, often basal to clusters of peripheral laterals; normally two support cells, occasionally only one; carpogonial branch of variable form, but usually straight; trichogyne shape and size variable, with various swellings and usually divided distally, 50 to 200 μm in length; each auxiliary cell producing two single-celled gonimoblasts and a single gonimolobe from each gonimoblast cell; mature gonimolobes rounded, not lobed; carposporangia variable in shape, due to appression, 25–45 μm in diameter.

Tetrasporangia spherical to ellipsoid, sessile, $60 \pm 8 \times 52 \pm 7$ μm, borne adaxially on peripheral laterals, rarely more than one per cell.

The overall thallus form of *Callithamnion tetragonum* is usually pyramidal and quite characteristic, only rarely appearing straggly and irregular. The peripheral laterals exhibit varying degrees of curvature and cell form, the extremes having been sufficiently distinct for two species to have been recognized formerly, although now treated merely as forms. In some thalli, the laterals are strongly incurved (*tetragonum* form; Price, 1978 : Fig. 13), whilst in others they are rather straighter and much narrower (*brachiatum* form; Price, 1978 : Fig. 14A): mixtures of the two types are also known.

Reproductive phenology in *Callithamnion tetragonum* is variable with location, year and individual thalli, but patterns can be perceived. Detailed information is being published elsewhere.

Ecology and distribution

Occurs in rock pools or open damp conditions at all levels, except high littoral and supralittoral, but best developed in the lower littoral under conditions of considerable, but not extreme, wave action, and in the sublittoral to 24 m; predominantly epiphytic, more rarely epilithic. Usually more abundant and luxuriant from the shallow sublittoral, especially on the laminae of *Laminaria* spp.

British Isles: Channel Islands, Cornwall, Devon, Somerset, Dorset, Hampshire, Isle of Wight, Sussex, Kent, Yorkshire, Durham, Northumberland, Isle of Man; Glamorgan, Pembroke, Cardigan, Caernarvonshire, Anglesey, Denbigh; Bute, Argyll, Ross & Cromarty, Orkney, Aberdeen, Angus, Fife, East Lothian, Berwick; Derry, Down, Antrim, Dublin, Wexford, Waterford, Cork, Kerry, Clare, Galway, Mayo.

World: North-eastern Atlantic from Iceland and Norway to the Algarve; Mediterranean; eastern coast of U.S.A. Recorded, possibly in error, from the Canaries, Cape Verde Islands, and the Cape of Good Hope.

Observations

Callithamnion tetragonum is not easy to mistake; even so, there have been numerous misidentifications.

Little information is available on the life history of *Callithamnion tetragonum*. Life history of the American *C. baileyi*, considered by some to be conspecific with *C. tetragonum*, has recently been elucidated by Whittick & West (1979). Chromosome counts $n = 9$–10, $2n = 18$–20 (Mathias 1927, 1928, 1932, 1935) were shown to be erroneous by Westbrook (1930*a*, 1935); $n = 28$–33 (Harris, 1962).

10. **Callithamnion tetricum** (Dillwyn) S. F. Gray, *Nat. Arr. Br. Pl.* **1** : 324 (1821).

Conferva tetrica Dillwyn, *Br. Conf.* : pl. 81 (1806).
Ceramium congestum Bonnemaison in *Mém. Mus. Hist. nat. Paris* **16** : 125 (1828).

Thallus red to brown in colour, rarely purple; rope-like, coarse and straggly, to 250 mm in height; main axes and major laterals densely corticate, cortication giving rise to very thick matrix of adventitious laterals; main axes 2–4 mm in breadth; branching strictly monopodial, indeterminate branches irregular in position and development, resembling main

axes; distal middle order laterals bearing stiff, shorter but progressively lengthening peripheral laterals giving a 'conical' (narrow pyramidal) outline to the individual branching system, the lower few cells of these distal and larger peripheral laterals occasionally bare; higher (later) order laterals distichous, angle of insertion acute, 50–60°; apical cells of bearing indeterminate laterals never over-topped by peripheral laterals (see Price, 1978 : Fig. 12); apical cells 125–175 μm near base of thallus, 75–100 μm behind distal apices of thallus; cell length-to-breadth ratios 1–3 (–5) to 1 in apical parts, (1–) 3–5 to 1 in basal parts of thallus; cells lengths and breadths increasing rapidly for about 4 to 6 cells behind the apical cell and immediate derivatives; chloroplasts irregular, discoid, or ribbon-shaped.

Gametangial phase dioecious. Spermatangiophores branched, branches 3–5 celled, borne on every cell of peripheral lateral, in luxuriant development forming large coalescent masses; 2–4 spermatangia from ultimate cells of spermatangiophores; spermatangia 4–8 μm.

Procarps formed behind apices, especially of peripheral laterals; usually two bilateral support cells, occasionally only one; carpogonial branch straight, less often zigzag; each central cell developing two 1-celled gonimoblast filaments which bear 1 gonimolobe each; mature gonimolobes with no subsidiary lobing; carposporangia 8–12 μm in diameter.

Tetrasporangia globose, 65–90 × 75–90 μm, sessile, adaxial on peripheral laterals, one per cell; bi- and tri-sporangia reported (Westbrook, 1930).

Habit varies little. Specimens more straggly over the winter and branching sparser and more open in sublittoral material. Perennial at least at times in Britain and probably throughout range. Branching pattern correlates with reproductive state, but seasonal effects probably equally as great.

Reproductive phenology in *Callithamnion tetricum* is variable with location, year and individual thalli, but patterns can be perceived. Detailed information is being published elsewhere.

Ecology and distribution

Usually epilithic or less commonly epiphytic on shores exposed to strong wave-beat, but never on the fully exposed positions that encourage especially *Callithamnion sepositum* and to a lesser extent *C. granulatum* on very exposed shores; *C. tetricum* occurs only in shore conditions offering some protection from direct wave impact (see Price, 1978).

British Isles: Channel Islands, Cornwall, Devon, Dorset, Hampshire (Isle of Wight), Kent, Norfolk (doubtful), Isle of Man; Glamorgan, Pembroke, Anglesey; Down, Dublin, Wexford, Waterford, Cork, Clare, Galway.

World: Known from north Ireland to Morocco.

Observations

Callithamnion tetricum, wherever it occurs, is one of the most distinctive species of the genus and has been involved in few confusions.

Little is known of the life history of *Callithamnion tetricum*. Reported chromosome numbers show curious disagreements. Westbrook (1930*b*) reported ?n = *c*.25 and ?2n = *c*.50, while Harris (1959) reported counts of 92, 93, 94 and 98 in sporangia, later cited (Harris, 1962) as '? 90–100'. The latter counts are three times greater than those obtained in any other species of *Callithamnion* and approximately twice the number reported by Westbrook.

Rejected species

1. Rejections from the British flora

Two species of *Callithamnion* accepted in the British flora for many years must be rejected, either on the grounds of taxonomic uncertainty or because of misidentifications. These are:

Callithamnion rabenhorstii (Kützing) P. Crouan & H. Crouan.

Described originally from the eastern Mediterranean (Ionian Sea) by Kützing (1849 : 896), the species was added to the British flora on the basis of material collected by E. M. Holmes at Studland (Dorset). The status of the entity is questionable, even at its original location, and there is no valid reason to accept the species in the British flora. Harris (1966) has suggested that the Holmes material resembles *C. byssoides*, and this attribution appears to be correct.

Callithamnion tripinnatum C. Agardh

This entity has been accepted in the British flora for many years, although it has been the subject of much confusion. The initial record for the British Isles, by Harvey (in Hooker, 1833 : 346), is based on material of *Compsothamnion* sp. Subsequently, Harvey (1847, pl. LXXVII) corrected this initial error, although the plants to which the name was then applied are referable to *Callithamnion hookeri*. Whatever the status of the original material of *C. tripinnatum* might be, as stated on p. 123 it would seem to form part of the *C. hookeri* assemblage; there is no valid reason for accepting *C. tripinnatum* in the British flora.

2. Entities of uncertain attribution

Several species, attributable to the genus *Callithamnion* and described from the shores of the British Isles and adjacent regions, cannot be referred with certainty to any of the previously mentioned species. There are two principal reasons for this uncertainty:

1. The type material cannot now be located, if it ever was preserved.
2. The type material has been located, but is inadequate in quality or quantity for determination.

The entities of uncertain attribution are:

Callithamnion arachnoideum Griffiths ex Moore in Larcom, *Ord. Surv. Londonderry* **1** : 11 (1837).
Callithamnion bipinnatum P. Crouan & H. Crouan, *Fl. Finistère* : 136 (1867).
See comments on pp. 123; 131.
Callithamnion caudatum J. Agardh in *Linnaea* **15** : 46 (1841).
Ceramium felicii Bonnemaison in *Mém. Mus. Hist. nat. Paris* **16** : 129 (1828).
Ceramium tetricum β pectinatum C. Agardh, *Syst. Alg.*: 141 (1824).

3. Rejections from the genus

In a few cases, examination of type material has disclosed that the entities in question must be rejected from the genus *Callithamnion*. For each, the reason for rejection is stated:

Callithamnion fallax P. Crouan & H. Crouan

Type locality: rade de Brest (Crouan & Crouan, 1867 : 135).
Holotype: CO*, Brest, 27 December 1856.
Comments: the holotype consists of depauperate scraps of *Antithamnion* sp.

Callithamnion parvulum P. Crouan & H. Crouan

Type locality: 'Sur le Codium spongiosum . . . rade de Brest' (Crouan & Crouan, 1867 : 135).
Holotype: CO, Crouan, Brest, 4 March 1858.
Other material: LD, Herb. Alg. Agardh 17973, possibly a duplicate of the holotype.
Comments: the holotype has the aspect of *Spermothamnion*, rather than *Callithamnion*, and terminal procarps are present.

*Abbreviations relating to herbaria are listed in the acknowledgements (pp. 138–139).

Callithamnion tetricum γ minus C. Agardh

Type locality: Pornic, coll. Desvaux (C. Agardh, 1828 : 180)
Holotype: LD, Herb. Alg. Agardh 18514.
Comments: the specimen is of *Pleonosporium borreri,* as was suggested by J. Agardh (1851 : 53).

Typifications

An attempt has been made to typify every name relevant to the present study. The results are listed in alphabetical order, initially by genus and then by species.

Callithamnion acrospermum J. Agardh

Type locality: 'in Oceano atlantico ad oras Galliae' (J. Agardh, 1851 : 52).
Lectotype: LD, Herb, Alg. Agardh 18295.
Other material: LD, Herb. Alg. Agardh 18296..

Callithamnion affine Harvey

Type locality: Bute, coll. Greville (Harvey in Hooker, 1833 : 344).
Lectotype specimen: TCD, Greville, Bute, undated, annotated 'Plant of Br. Flora H' in Harvey's hand.
Other material: TCD, three specimens. BM(K), one specimen.

Callithamnion arachnoideum C. Agardh

Type locality: 'in mari Atlantico ad Noveboracum, unde misit Torry' (C. Agardh, 1828 : 181).
Lectotype: LD, Herb. Alg. Agardh 18435.
Other material: LD, Herb. Alg. Agardh 18436 [mica preparation, probably of 18435], 18443.

Callithamnion arachnoideum Griffiths ex Moore, *nom. illeg.*

Type locality: 'near the mouth of the Bann' (Moore, 1837 : 11).
Type material: it has not been possible to locate any original material.

Callithamnion arnottii Trevisan, *nom. illeg.*

Comments: *C. arnottii* (as '*C. Arnotti*') was proposed by Trevisan (1845 : 77) as a substitute name for *C. byssoides.* It is, therefore, a superfluous and illegitimate name which must be typified by the type of *C. byssoides* (q.v.).

Callithamnion bipinnatum P. Crouan & H. Crouan

Type locality: rade de Brest (Crouan & Crouan, 1867 : 136).
Lectotype: CO, Crouan, rade de Brest, Aug. 1850.
Other material: CO, 3 specimens.
Comments: for discussion of the possible status of this taxon in different parts of Europe, see Price (1978) and Rueness & Rueness (1980).

Callithamnion brodiaei Harvey

Type localities: Forres, Coll. Brodie; Northumberland, coll. Robertson; Torquay, coll. Griffiths & Cutler (Harvey in Hooker, 1833 : 340).

Lectotype: TCD, Brodie, Lossiemouth, undated, annotated as 'authentic' in Harvey's hand.

Other material: TCD, three specimens. LD, Herb. Alg. Agardh 19018, 19025. GL, two specimens.

Comments: the original treatment contains two curious misstatements. The Brodie specimens were collected at Lossiemouth according to Brodie's annotations, not at Forres, which was where he lived and is a few kilometres from the sea. The Northumberland specimen is annotated as having been collected by 'Mr. Robinson', whereas the collector was quoted as 'Mr. Robertson' in the published text.

Callithamnion byssoides Arnott ex Harvey

Type localities: 'Whitsand bay, G.A.W. Arnott, Esq. Devonshire, Mrs. Griffiths' (Harvey in Hooker, 1833 : 342).

Lectotype: TCD, Arnott, Whitsand Bay, 1829, annotated 'original plant of Br. Flora WHH' (in Harvey's hand).

Other material: TCD, one specimen. LD, Herb. Alg. Agardh 18407. GL, seven specimens, possibly duplicates.

Callithamnion caudatum J. Agardh

Type locality: 'in mari mediterraneo ad littora Galloprovinciae; rupibus insulae St. Marguerite' (J. Agardh, 1841 : 46).

Lectotype: LD, Herb. Alg. Agardh 18386.

Other material: LD, Herb. Alg. Agardh 18390. Numerous other specimens exist (BM, TCD, etc.), distributed by J. Agardh, but it would seem best to exclude these because of doubts as to their provenance.

Callithamnion decompositum J. Agardh

Type locality: 'in oceano atlantico ad oras Galliae' (J. Agardh, 1851 : 45).

Holotype: LD, Herb. Alg. Agardh 18964.

Comments: this entity is often attributed, partly or completely, to Grateloup, due to a misinterpretation of the comment by J. G. Agardh that Grateloup had given the manuscript name *Mertensia decomposita* to the specimen used as the basis for the original treatment.

Callithamnion fruticulosum J. Agardh

Type locality: 'in sinu Codano' (J. Agardh, 1841 : 46).

Lectotype: LD, Alg. Agardh 19047, bearing TYPUS slip attributed to T. Levring.

Other material: LD, Herb, Alg. Agardh 19046, 19048. TCD, J. Agardh, undated, a mica preparation in a packet annotated '*Callith. fruticulosum* Ag. MSCR e sinu Codano J. Agdh.' in J. Agardh's hand.

Callithamnion furcellariae J. Agardh

Type locality: 'in *Furcellaria* parasiticum ad oras Bahusia' (J. Agardh, 1851 : 37).

Lectotype: LD, Herb. Alg. Agardh 19087.

Other material: LD, Herb. Alg. Agardh 19088, 19089.

Comments: a TYPUS label has been attached to Herb. Alg. Agardh 19085, but it is not clear why this was selected because it makes reference to *Solenia*, not *Furcellaria*, which *is* cited on the specimen cited above as lectotype.

Callithamnion grande J. Agardh

Type locality: 'ad rupes insularum Stoechadum' (J. Agardh, 1842 : 73).

Holotype: LD, Herb. Alg. Agardh 19277.

Callithamnion grevillei Harvey

Type localities: 'Firth of Forth, Dr. Greville, Berwick, Dr. Johnston' (Harvey in Hooker, 1833 : 345).

Lectotype: TCD, Greville, no locality, undated, a packet containing a mica preparation, annotated 'Plant of Br.Fl.' in Harvey's hand.

Callithamnion harveyanum J. Agardh

Type localities: *Callithamnion harveyanum* was first used by J. Agardh (1841 : 45), who claimed that the plant treated by Harvey under the name *Callithamnion granulatum* was distinct from that taxon. As J. Agardh did not provide a formal diagnosis, the original description must be that given by Harvey, and the type localities those quoted by the latter, viz. Appin [in error, cf. comment below], coll. Carmichael; Whitsand Bay, coll. Arnott.

Lectotype: TCD, Carmichael, Staffa, July 1826, annotated 'Specimen described in British Flora as *C. granulatum* is not that plant WHH' in Harvey's hand.

Other material: LD, Herb. Alg. Agardh 18339.

Comments: the lectotype and the LD specimen are both annotated to indicate that they were collected by Carmichael at Staffa, not Appin, as indicated in the Harvey treatment.

Callithamnion hiemale Kjellman ex Kylin

Type locality: Kristineberg (Kylin, 1907 : 170).

Holotype: LD, Kylin, Kristineberg, 9 December 1905.

Callithamnion lanosum Harvey

Type localities: 'Tor Abbey, Mrs. Griffiths. Killiney, W. H. Harvey' (Harvey in Hooker, 1833 : 341).

Lectotype: TCD, Harvey, Killiney, undated.

Other material: TCD, four specimens. BM, one specimen. LD, Herb. Alg. Agardh 18257, 18258.

Comments: Harris (1966) cited the type locality for this entity as 'Beach below Tor Abbey, Menai Straits, N. Wales', a geographically meaningless aggregation of localities that bears no relation to the original treatment.

Callithamnion octosporum C. Agardh

Type locality: 'Ad litora Galliae maris Atlantici, ut ad Port Louis' (C. Agardh, 1828 : 177).

Holotype: LD, Herb. Alg. Agardh 18493.

Other material: LD, Herb. Alg. Agardh 18492, a mica preparation apparently derived from 18493.

Callithamnion polyspermum C. Agardh

Type locality: 'Ad Finisterre Galliae, unde misit Bonnemaison' (C. Agardh, 1828 : 169).

Holotype: LD, Herb. Alg. Agardh 18236.

Other material; LD, Herb. Alg. Agardh 18235, a mica preparation apparently derived from 18236. PC, F, QUI, several specimens occur which may possibly represent duplicates of the holotype indicated above, since they were received from Bonnemaison and referred by him, as was the holotype, to '*Lamourouxia polysperma*' (a *nomen nudum*).

Callithamnion pseudobyssoides P. Crouan & H. Crouan

Type locality: 'sur le *Plocaria confervoides* . . . Kervallon' (Crouan & Crouan, 1867 : 136).

Lectotype: CO, Crouan, Kervallon, undated.

Other material: CO, one specimen. LD, Herb. Alg. Agardh 18426.

Callithamnion roseum β **tenue** Lyngbye

Type locality: Faeroe (Lyngbye, 1819 : 126).
Lectotype: LD, Herb. Alg. Agardh 18997.
Other material: LD, Herb. Alg. Agardh 18994. C, Lyngbye, 'Hoyviig prope Thorshavn Faeroe', 11 June 1817. PC, Lyngbye, Faeroe, undated, labelled '*Callithamnion roseum β tenue',* in Lyngbye's hand.
Comments: Lyngbye and C. Agardh obviously exchanged material extensively; C. Agardh made use of exchange material as the basis for both *Ceramium scopulorum* and *Callithamnion scopulorum* (q.v.).

Callithamnion scopulorum C. Agardh

Type locality: Faeroe (C. Agardh, 1828 : 166).
Lectotype: LD, Herb. Alg. Agardh 18997.
Other material: LD, Herb. Alg. Agardh 18994. C, Lyngbye, 'Hoyviig prope Thorshavn Faeroe', 11 June 1817. PC, Lyngbye, Faeroe, undated, labelled '*Callithamnion roseum β tenue'* in Lyngbye's hand.
Comments: as discussed under *Callithamnion roseum β tenue* (q.v.), C. Agardh made use of Lyngbye exchange material of the latter entity as the basis for *Callithamnion scopulorum.* The original treatment of the latter quoted '*Callithamnion roseum tenue* Lyngb.' in its synonymy, although there is no mention of *Ceramium scopulorum* (q.v.), which had already been based (C. Agardh, 1824) on the same material.

Callithamnion spiniferum Kylin

Type localities: Hogardsgrund, Varberg, Morup (Kylin, 1907 : 159).
Lectotype: LD, Kylin, Morup, 21 February 1903.
Other material: LD, Kylin, Hogardsgrund, 6 July 1907.

Callithamnion spinosum Harvey

Type locality: Sidmouth, coll. Griffiths (Harvey in Hooker, 1833 : 345).
Holotype: TCD, Griffiths, Sidmouth, undated, annotated 'Cal. spinosum H. in Br. Flora. Sent by Mrs. Griffiths to Dr. Greville from Sidmouth—my only specimen' in Harvey's hand.
Comments: Harris (1966) cited as holotype a specimen at TCD, undefined as to locality and lacking further identifying data. That specimen is of no importance to the correct typification.

Callithamnion spongiosum Harvey

Type localities: Torquay, coll. Griffiths; Kingston, coll. Harvey; Killiney, coll. Harvey (Harvey in Hooker, 1833 : 346).
Lectotype: TCD, Griffiths, Meadfoot (Torquay), June 1832.
Other material: TCD, five specimens. BM, two specimens. BM(K), one specimen. GL, one specimen. LD, Herb. Alg. Agardh 19249.

Callithamnion tetragonum β **firmius** C. Agardh

Type locality: 'Frishwater [sic] Bay' (C. Agardh, 1828 : 176).
Holotype: LD, Herb. Alg. Agardh 18341.
Other material: LD, Herb. Alg. Agardh 18342, a mica preparation apparently prepared from 18341.

Callithamnion tripinnatum C. Agardh

Type locality: '*Mertensia tripinnata* Gratel. Msct. In Mari Atlantico, unde specimen misit Grateloup' (C. Agardh, 1828 : 168).

Holotype: LD, Herb. Alg. Agardh 18975.

Comments: citation of the authority is confused. Direct attribution to Grateloup is incorrect as his name is a *nomen nudum*, while citation in the form 'Gratel. ex. C. Ag.' is also incorrect in that C. Agardh took up only the epithet and not the whole binomial from Grateloup (see *International Code of Botanical Nomenclature*, Recommendation 46C.1).

Ceramium brachiatum Bonnemaison, *nom. illeg.*

Comments: the original treatment (Bonnemaison, 1828 : 136) made reference to collections from three localities on the Atlantic or Channel coasts of France, to another from the Mediterranean, and to two specimens collected in the Canary Islands and at the Cape of Good Hope. More significantly, it placed in synonymy binomials which lead back to *Conferva tetragona* Withering and made no mention of the latter elsewhere in the text, so that these synonyms must be taken as references to type. There is no option but to dismiss *Ceramium brachiatum* as a superfluous and illegitimate name which must be typified by the type of *Conferva tetragona*.

Ceramium congestum Bonnemaison, *nom. illeg.*

Comments: the original treatment (Bonnemaison, 1828 : 125) made reference to collections from nine localities on the Channel and Atlantic coasts of France. The critical feature of the treatment is that it placed in the synonymy *Conferva tetrica* Dillwyn (1806). On the basis of that citation, one must dismiss *Ceramium congestum* as a superfluous and illegitimate name, to be typified by the type of *Conferva tetrica*.

Ceramium dudresnayi Bonnemaison, *nom. illeg.*

Comments: the original treatment (Bonnemaison, 1828 : 125) made reference to various specimens but also to several previously-published binomials, of which the oldest is *Conferva purpurascens* Hudson. Therefore *Ceramium dudresnayi* is a superfluous and illegitimate name which must be typified by the type of *Conferva purpurascens*.

Ceramium felicii Bonnemaison

Type locality: 'Dieppe' (Bonnemaison, 1828 : 129).

Lectotype: PC, Gaillon, Dieppe, undated, annotated as '*Ceramium felicii* Gaillon mnscr' in Bonnemaison's hand.

Other material: specimens were distributed widely by Gaillon, although he never provided a description. The greatest number were issued as specimen 203 of Desmazière's '*Plantes Cryptogames*' but others, not from this source, occur at CO (ex Crouan) and at LD (Herb. Alg. Agardh 19016, also ex Crouan).

Ceramium fruticulosum Roth

Type locality: not stated (Roth, 1800 : 183), but as the original material was collected by Wulfen it was probably from the Adriatic.

Type: typification is not currently possible as there is no evidence at either B or W to indicate that the original material is still in existence and no illustration is provided.

Comments: Roth (1800) compared his alga with *Conferva marina nodosa* of Dillenius (1741), the type of *Conferva purpurascens* Huds., and in a later treatment (Roth, 1806 : 147) actually cited the latter in his treatment of *Ceramium fruticulosum.* Wulfen (1803) independently described *Conferva fruticulosa* (q.v.), and it is probable that the two entities are based on fragments of the same original gathering.

Ceramium granulatum Ducluzeau

Type locality: Sette (Ducluzeau, 1806 : 72).

Type: typification is not currently possible as nothing is known of the location of any Ducluzeau material and no illustration, although announced, is provided with the original treatment.

Ceramium guttatum Bonnemaison

Type localities: Penmark, Cherbourg (Bonnemaison, 1828 : 137).
Lectotype: PC, locality not indicated, Bonnemaison, undated, labelled '*Ceramium guttatum* B^nsp. nov.', in Bonnemaison's hand, and filed under *Callithamnion tetragonum*.

Ceramium roseum Roth

Type locality: Bayonne (Roth, 1798 : 47).
Type: indisputable type material not located. Neotype designated below.
Comments: the existence of Roth's herbarium is at present a matter of doubt. Usually, it is assumed to have been lost in the bombing of the Berlin-Dahlem Museum (Pilger, 1953); this seems true of specimens of *Ceramium roseum*. There is a specimen at LD (Herb. Alg. Agardh 18466), labelled '*Ceramium roseum* Roth Bayonne dedit Roth ipse non *rosea* Dillw' in C. Agardh's hand, but the status of this is uncertain. Subsequent interpretations (Dillwyn, 1802; Smith, 1802) were based on a specimen collected in 1797 by Sowerby at Yarmouth and sent to Roth for comment by Dawson Turner. This specimen, which Roth identified as '*Ceramium roseum*', passed to K (now at BM), with a duplicate of the original Sowerby collection at BM. Although not part of the type collection, these specimens help to unravel subsequent interpretations of this taxon, of which there have been several. This K(BM) specimen is here designated as of neotype status.

Ceramium scopulorum C. Agardh

Type locality: Faeroe (C. Agardh, 1824 : 132).
Lectotype: LD, Herb. Alg. Agardh 18997.
Other material: C, Lyngbye, 'Hoyviig prope Thorshavn Faeroe', 11 June 1817. PC, Lyngbye, Faeroe, undated, labelled '*Callithamnion roseum tenue*' in Lyngbye's hand.
Comments: as discussed under *Callithamnion roseum β tenue* (q.v.), Lyngbye and C. Agardh exchanged material and C. Agardh made use of material of the latter entity as the basis for *Ceramium scopulorum*. The original treatment of the latter quoted '*Callithamnion roseum tenue*, Lyngb.' in its synonymy. The same material was later used by C. Agardh as the original material for *Callithamnion scopulorum* (q.v.), although the latter description makes no reference to the earlier *Ceramium scopulorum*.

Ceramium tenuissimum Bonnemaison

Type localities: St-Pol-de-Léon, Brest, St. Malo (Bonnemaison, 1828 : 132).
Provisional lectotype: PC, Bonnemaison, no locality, undated, annotated '*Ceramium tenuissimum* B^n' in Bonnemaison's hand, filed as *Seirospora tenuissimum*.
Comments: despite widespread search at QUI, it was not possible to locate any authentic material in what remains of Bonnemaison's herbarium. Presumably the specimen cited above as provisional lectotype is that referred to by Harris (1966).

Ceramium tetricum β pectinatum C. Agardh

Type locality: 'Ad oras Galliae, Africae Borealis' (C. Agardh, 1824 : 141).
Lectotype: LD, Herb. Alg. Agardh 18307.
Other material: LD, Herb. Alg. Agardh 18309.

Ceramium versicolor C. Agardh *nom. illeg.*

Comments: the original treatment (C. Agardh, 1824 : 140) cites three previously published binomials, one identification, and the manuscript source of the epithet. Despite widespread search, we have been unable to locate the type material of any of the previous binomials. *Ceramium versicolor* is a superfluous and illegitimate name, incapable of typification, which must be dismissed from consideration.

Conferva arbuscula Dillwyn

Type localities: Ballycastle, coll. Brown; Bantry Bay, coll. Hutchins (Dillwyn, 1807, pl. 85).

Lectotype: BM(K), ? Brown, North coast of Ireland, undated.

Other material: BM, 2 specimens. GL, 2 specimens.

Comments: the typification has been discussed in detail by Dixon (1960, 1964). The choice of lectotype was made on the basis of the statement by Dillwyn (1809 : 35) that Dawson Turner provided the original description of the entity. The position became confused as a consequence of a later figure (Dillwyn, 1809, pl. 6G) based on a specimen of *Dasya*, so that the epithet *arbuscula* came to be applied in both *Callithamnion* and *Dasya.* Despite previous resolution of this problem (Dixon, 1960, 1964), Harris (1966) stated that he had been unable to locate original material.

Conferva corymbosa Smith

Type localities: Brighthelmstone [=Brighton], coll. Borrer; Kingsbridge, coll. Gibbs; Bantry Bay, coll. Hutchins (Smith, 1811, pl. 2352).

Lectotype: BM, Borrer, Brighton, July 1811.

Comments: Harris (1966) quoted the type locality as Kingsbridge and cited as holotype a specimen 'in the British Museum of Natural History, no. 271'. The original treatment is based on three collections, so that holotype status for any specimen is impossible. It would appear that this author was misled by the seven irrelevant specimens, in the type folder at BM, mounted on the same sheet as the Borrer specimen. The specimen cited by Harris is an example from '*Algarum Fasciculi*' distributed by J. Cocks, and has no relevance whatsoever to the typification of *Conferva corymbosa.*

Conferva fruticulosa Wulfen

Type locality: 'Insulae Gradensis' (Wulfen, 1803 : 26).

Type: typification is not currently possible as the original material cannot be located, and no illustration is provided with the original treatment.

Comments: Wulfen stated that his material was similar to the illustration of *Conferva marina nodosa* of Dillenius (1742). Roth (1800) described *Ceramium fruticulosum* on the basis of material supplied by Wulfen and also commented on the relationship to the same Dillenian entity. *Conferva fruticulosa* Wulfen and *Ceramium fruticulosum* Roth are independent names, based on different types, although these are probably fragments of the same original gathering.

Conferva hookeri Dillwyn

Type localities: Cawsie, coll. Hooker and Borrer; Holyhead, coll. Davies; Bantry Bay, coll. Hutchins (Dillwyn, 1809 : pl. 106).

Lectotype: TCD, Hooker and Borrer, Cawsie, undated, labelled 'Br. Flora C. Hookeri Cawsie Hook. Borrer', in Harvey's hand.

Other material: BM(K), three specimens.

Comments: Harris (1966) cited a K specimen, supposedly from Holyhead, Anglesey. None of the K material mentioned above is so annotated and the specimen at TCD is the legitimate choice of lectotype.

Conferva purpurascens Hudson

Type locality: unspecified (Hudson, 1778 : 600).
Holotype: OXF, Dillenian material of *Conferva marina nodosa*.
Comments: Hudson's description is based exclusively on the plant described previously by Dillenius (1742) as *Conferva marina nodosa* . . . Harris (1966) came to a similar conclusion, although he considered the Dillenian material as of neotype status. Although Hudson cited no precise locality in his treatment of *Conferva purpurascens*, Dillenius (1742 : 36) indicates that his material was collected near 'Lhanfaethly', Anglesey, which is therefore the type locality for the Hudson taxon.

Conferva seposita Gunnerus

Type localities: 'ad Hoburgam Gotlandiae; in mari sundmorico [near Alesund, Norway]; prope Lhanfaethly in Mona Insula [Anglesey]' (Gunnerus, 1772 : 116).
Lectotype: OXF, Green, Lhanfaethly, undated, in Dillenius's *Historia Muscorum* herbarium.
Comments: the lectotype selected is also the lectotype of *Conferva purpurascens* Hudson (q.v.).

Conferva tetragona Withering

Type locality: 'found by Major Velley and Mr. Stackhouse at the Bill of Portland' (Withering, 1796 : 405).
Provisional lectotype: GL, Velley, Isle of Portland, undated.

Conferva tetrica Dillwyn

Type locality: 'Common about the Mumbles and in other parts of the Peninsula of Gower' (Dillwyn, 1806, pl. 81).
Lectotype: WELT, Herb. Silvanus P. Thompson A 4502, Dillwyn, Swansea, 1806.

Ellisius glaber S. F. Gray, *nom. illeg.*

Comments: *E. glaber* is a superfluous and illegitimate name, in that *Conferva arbuscula* Dillw. is cited as a synonym (Gray, 1821 : 333). The genus *Ellisius* was established with two species, *E. glaber* and *E. coccineus,* the latter based on *Conferva coccinea* Hudson [= *Heterosiphonia plumosa* (Ellis) Batters]. *Heterosiphonia* Montagne (1842) has been conserved against *Ellisius*.

Phlebothamnion faroense Kützing

Type locality: 'Faeroe' (Kützing, 1864 : 30).
Holotype: L, Herb. Lugd. Bat. 940.237.116, Lyngbye, Faeroe, undated.

Phlebothamnion scoticum Kützing

Type locality: Aberdeen (Kützing, 1864 : 30).
Holotype: L, Herb. Lugd. Bat. 940.237.118, Dickie, Aberdeen, June 1843.

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Addendum

Since this paper went to press the following references have come to the authors' attention.

Hoek, C. van den (in press). Distribution groups of benthic marine algae in relation to the temperature regulation of their life histories. *In* J. H. Price, R. W. Sims & P. E. S. Whalley, *Evolution, Time and Space : the Emergence of the Biosphere.* London.

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Parmelia subgenus *Amphigymnia* (lichens) in East Africa

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Contents

Synopsis

Seventy species of *Parmelia* subgenus *Amphigymnia* (Vainio) Dodge are reported from East Africa, their ecology and distribution discussed, and a key and descriptions to the species are provided. The following new species are described: *Parmelia aprica, P. durumae, P. jacarandicola, P. kwalensis, P. leonis, P. pardii, P. pigmentifera, P. rava, P. taitae, P. tsavoensis, P. umbrosa,* and *P. vivida.* The new name *Parmelia indoafra* is proposed for *Parmotrema indicum* Hale, non *Parmelia indica* Sprengel. The following taxa are reduced to synonymy: *Parmelia aberrans* (Vainio) des Abb., *P. madagascariacea* (Hue) des Abb., and *P. nyasensis* Dodge with *P. xanthina* (Müll. Arg.) Vainio; *Parmelia affluens* Hale with *P. dilatata* Vainio; *Parmelia balensis* Winnem, *P. neolobulascens* Winnem, and *Parmotrema subcompositum* Hale with *Parmelia subschimperi* Hale; *Parmelia breviciliata* Hale and *P. procera* Steiner & Zahlbr. with *P. maclayana* Müll. Arg.; *Parmotrema conferendum* Hale and *Parmelia leucosemotheta* Hue with *P. subsumpta* Nyl.; *Parmelia composita* Hale and *P. spilota* Hale with *P. euneta* Stirton; *Parmelia deflectens* Kurok. with *P. subarnoldii* des Abb.; *Parmelia diversa* Hale with *P. nilgherrensis* Nyl.; *Parmelia modesta* Hue with *P. andina* Müll. Arg.; *Parmelia mordenii* Hale with *P. praesorediosa* Nyl.; *Parmelia natalensis* Steiner & Zahlbr. and *P. pseudonilgherrensis* Asah. with *P. lobulascens* Steiner; *Parmelia pachyspora* Hale with *P. amaniensis* Steiner & Zahlbr.; *Parmelia paradoxa* Hale with *P. inexpectata* des Abb.; *Parmelia pseudoreticulata* Tavares and *P. simulans* Hale with *P. reticulata* Taylor; *Parmelia pseudotinctorum* des Abb. with *P. tinctorum* Nyl.; and *Parmelia virens* Müll. Arg. with *P. erubescens* Stirton. *Parmelia consors* Nyl. and *P. pilosa* Stizenb., previously classified in genus *Parmelina* Hale, are here included in subgenus

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Amphigymnia (genus *Parmotrema* Massal.). The generic concept and infrageneric classification are briefly discussed.

Introduction

Previous collections and research

Species of *Parmelia* subgenus *Amphigymnia* (Vainio) Dodge form one of the major dominant groups of lichens in East Africa. Being large and conspicuous they were frequently collected by both botanists and non-botanists on various expeditions during the 19th century. New species and infraspecific taxa now classified in *Amphigymnia* were described by contemporary lichenologists (names in parentheses) from material brought back to Europe by the following collectors: Hannington (Müller, 1890), Hildebrandt (Krempelhuber, 1877, Müller, 1884, 1885), Holst (Müller, 1894), Liechtenstein & Pospischill (Steiner, 1897), Maclay (Müller, 1891), Meyer (Stein, 1888; Müller, 1890), Schimper (Müller, 1892), Scott Elliot (Vainio, 1898), Stuhlmann (Müller, 1893, 1894), Thomson (Stirton, 1877–78), and Volkens (Müller, 1894). Most of these new taxa, together with records of other lichens occurring in our area, were included in an account by Stizenberger (1890, 1891, 1893, 1895) of lichens known from Africa at that time.

In this century Jatta (1909) published an account of lichens from the Ruwenzori mountains, and Hue (1916) reported on lichens collected in Kenya by Vicomte de Poncins. Steiner & Zahlbruckner (in Zahlbruckner, 1926), Zahlbruckner (1932), and Zahlbruckner & Hauman (1936) published on various collections of lichens from the African continent. Several of them are pertinent to our area, especially those collected by Brunnthaler, as well as those by Fincke, Schröder, Tobler, and F. & R. Wettstein. Cengia Sambo (1937*a, b,* 1938, 1940) reported on lichens mainly from Ethiopia, but also from Kenya and Tanzania, and Klement (1962) published an account of a small collection of lichens from Tanzania made by Drs E. and R. Schüz.

Dodge (1953, 1959) studied those East African Parmelias lodged in the herbaria of EA, FH, and K (now in BM), describing a number of new species. His accounts include many species in *Amphigymnia* which are now accommodated elsewhere. Hale (1965) published a world monograph of the subgenus, reducing numerous taxa to synonymy and describing many new species. Nearly 30 of the species he treated were then known to occur in East Africa. In subsequent publications Hale (1972, 1973, 1977) described several additional species from our area. Winnem (1975) treated the 31 species of the subgenus *Amphigymnia* occurring in Ethiopia. A further two species have previously been discussed by the present authors (Krog, 1974; Krog & Swinscow, 1975). It is noteworthy that most of the authors cited were not familiar with the African lichen flora in the field. The main exception is Winnem (1975), who based her study of Ethiopian lichens on her own collections and a first-hand knowledge of the physiography of the country.

The aim of the present study is to give a comprehensive account of the species belonging to *Parmelia* subgenus *Amphigymnia* in East Africa. Special emphasis is placed on the circumscription of the species in the light of characters of the reproductive organs, new chemical data, ecological observations, and a knowledge of the variation within local populations.

Taxonomic review

Massalongo (1860) segregated the genus *Parmotrema* Massal., based on *Parmelia perforata* (Jacq.) Ach., from *Parmelia* Ach. Vainio (1890) introduced *Parmelia* subgenus *Euparmelia* sect. *Amphigymnia* Vainio with 11 species, but did not designate a type. Dodge (1959) raised the section to subgeneric level, noting that a type had not been designated. Hale (1965) treated the subgenus monographically and selected *Parmelia tinctorum* Nyl. as the lectotype for it. Hale (1974*b*) reintroduced genus *Parmotrema* Massal., including in it not only most of

the species which had previously been accommodated in subgenus *Amphigymnia* (Vainio) Dodge, but also the *P. reticulata* group, previously included in subgenus *Parmelia.*

Materials and methods

The following account is based mainly on collections made by the authors as follows: Uganda (T. D. V. S. 1969, 1970, 1971), southern Ethiopia (H. K. 1972), Kenya (H. K. & T. D. V. S. 1972, 1973, 1974, H. K. 1976, T. D. V. S. 1977), and northern Tanzania (H. K. & T. D. V. S. 1974). In addition to specimens in institutional herbaria we have been permitted to examine material collected in recent years by the following botanists: Lye (Uganda), Moberg (Kenya, Tanzania), Pócs (Tanzania), Santesson (Kenya, Tanzania), Sharp (Tanzania), Sipman (Kenya, Tanzania), and Vitikainen (Kenya). Specimens cited with a number but without a collector's name were collected by one of the authors. Specimens have been deposited in O, BM, and East African herbaria.

The material referred to in this study has been subjected to thin-layer chromatography (TLC) by means of standard methods (C. Culberson, 1972; Menlove, 1974). However, type specimens which have recently been tested by TLC have not been retested unless it was specially indicated. All specimens cited, including types, have been personally studied unless otherwise noted. In the text + denotes a low concentration of a given substance, whilst ± denotes its sporadic occurrence (accessory substance).

The descriptions of the species are based on East African material, and comprise only those morphotypes and chemotypes which occur in our area. Only selected East African records are given for the commoner species, but in such cases at least one record is chosen from each district (or, for Uganda, each county) in which the species has been collected. Only new or otherwise interesting synonyms are given. For a more complete citation see Hale (1965).

Results

Morphology

The apothecia of *Parmelia tinctorum,* the type species of the subgenus, are substipitate and laminal. But in the majority of East African species they were found to be submarginal to marginal, with swollen and inflated or more or less constricted but well developed stipes. At or near the lobe margin the stipe was sometimes formed by a semitubular fold of a convoluted lobe, and in such cases the disc might be eccentrically orientated in relation to its stipe.

In contrast to those of other subgenera in *Parmelia, Amphigymnia* species often have perforated apothecial discs. In some species the perforations were found to have developed at an early stage in nearly all the apothecia of a thallus, while in others they were present only in some of the apothecia of a given thallus or occurred sporadically and seemingly accidentally in old apothecia.

The spores were simple and ellipsoid and varied in length from 10 to 40 μm. With some individual variation, spore size in the subgenus could be roughly divided into three fairly well defined categories: (a) small, thin-walled, 10–20 (22) μm; (b) intermediate, usually relatively thick-walled, 20–28 μm; and (c) large, thick-walled, 25–40 μm. In the first group it was, to a certain degree, even possible to distinguish between species with spores less than *c.* 16 μm and those 16–20 (22) μm in length. Our own observations and previous reports show that the East African species could be divided by spore size into the four groups shown in Table 1. In sorediate species the spores were sometimes poorly developed and on the average smaller than in their non-sorediate counterparts.

The pycnidia were situated in a broad submarginal zone in all primary species, and were

Table 1 Approximate spore sizes in the East African species of *Parmelia* subgenus *Amphigymnia*.

10–16 (18) μm	16–20 (22) μm	20–28 (30) μm	25–40 μm
P. aldabrensis	*P. abessinica*	*P. dilatata*	*P. amaniensis*
P. cetrata	*P. andina*	*P. durumae*	*P. bangii*
P. erubescens	*P. austrosinensis*	*P. euneta*	*P. crinita*
P. eurysaca	*P. cooperi*	*P. inexpectata*	*P. cristifera*
P. grayana	*P. gardneri*	*P. lobulascens*	*P. cryptoxantha*
P. jacarandicola	*P. hababiana*	*P. nilgherrensis*	*P. eciliata*
P. maclayana	*P. hanningtoniana*	*P. perlata*	*P. subarnoldii*
P. pardii	*P. hololoba*	*P. subschimperi*	
P. reticulata	*P. leonis*		
P. sancti-angelii	*P. mellissii*		
P. soyauxii	*P. pigmentifera*		
P. stuhlmannii	*P. praesorediosa*		
P. subcolorata	*P. pseudocrinita*		
P. subisidiosa	*P. rava*		
P. subsumpta	*P. rimulosa*		
P. subtinctoria	*P. uberrima*		
P. taitae	*P. vivida*		
P. tinctorum	*P. zollingeri*		
P. ultralucens			
P. xanthina			

also found in this position in a number of secondary species. In modern taxonomic treatments of parmelioid lichens little emphasis has been placed on the conidia, although their shape and size were faithfully recorded by most earlier lichenologists as an important part of the descriptions of new species. Within some lichen genera there is obviously little variation between the species, but in *Parmelia s. lat.* the conidia were very variable and are therefore treated here in some detail.

In the Parmeliaceae the conidia are produced endobasidially on conidiophores of the bayonet type (Glück, 1899) (Fig. 1a). The development of the conidiophores, which has been discussed by Vobis (1980), is of little interest in the present study and is not treated here. As for the conidia, however, we have found that five common types can be recognized within the Parmeliaceae:

(*a*) *Bifusiform conidia.* The term has been applied by, for example, Esslinger (1977) and Vobis (1980), to short conidia, usually 4–6 (7) μm long, which are constricted in the middle with a swelling near but not at both ends (Fig. 1b). Other terms for this type are 'hantelförmig' and 'bisquitförmig' (Glück, 1899) and 'dumb-bell-shaped' (Kärnefelt, 1979). Within the Parmeliaceae we have observed bifusiform conidia in *Cetraria, Cetrelia, Hypogymnia,* and *Parmelia* subgenus *Hypotrachyna,* but never in subgenus *Amphigymnia.*

(*b*) *Sublageniform conidia.* The term has been used to denote short, rod-shaped conidia, 5–8 μm long, with a slight swelling near one end (Fig. 1c). Nylander (1885) applied the term to the conidia of *Parmelia corniculans*, and Steiner & Zahlbruckner (in Zahlbruckner, 1926) to those of *P. procera.* The term lageniform means flask-shaped, but since the swelling in this type of conidia is subterminal rather than terminal, the term sublageniform is adopted. We find this term more appropriate than Glück's choice 'keulig' or clavate (Glück, 1899). In some species the swelling is indistinct and may be discernible only in a few of the many conidia from a pycnidium, while the rest may appear rod-shaped. In the Parmeliaceae *sensu* Henssen & Jahns (1973) sublageniform conidia occur in, for example, *Usnea* (Swinscow & Krog, 1976, Fig. 7), *Letharia*, *Platismatia*, and *Parmelia* subgenus *Amphigymnia pro parte.*

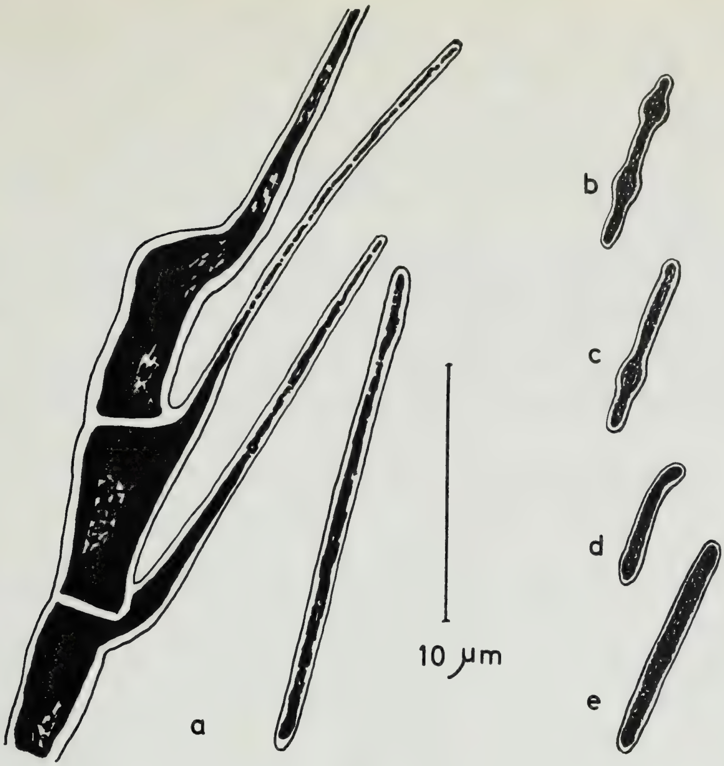

Fig. 1 Conidia in genus *Parmelia* s. lat. **a**: conidiophore with filiform conidia, *P. euneta* Stirton, 3K 16/122. **b**: bifusiform conidium, *P. ducalis* Jatta, E 30/12. **c**: sublageniform conidium, *P. maclayana* Müll. Arg., *Ryvarden* 9032. **d**: unciform conidium, *P. subpraesignis* Nyl., T 16/137. **e**: rod-shaped conidium, *P. eciliata* (Nyl.) Nyl., 4 May 1978, *Dahl* s.n.

Sublageniform conidia with one or two darker 'dots' (see below under rod-shaped conidia) have been seen in the subgenus *Everniiformes*.

(*c*) *Unciform conidia.* We have chosen this term to denote rod-shaped conidia *c.* 5 μm long, with a single hook-shaped end (Fig. 1d), a type not discussed by Glück (1899) or Vobis (1980). They are particularly characteristic for *Parmelia* subgenus *Parmelia* sect. *Simplices*, occurring in all the species examined by us, with the exception of *P. microsticta* Müll. Arg. and *P. hypoleucites* Nyl *s. str.* in which they were filiform (see also W. Culberson & C. Culberson, 1980). The presence of unciform conidia in *Amphigymnia* has not been conclusively proved.

(*d*) *Rod-shaped (bacilliform) conidia.* This is a rather heterogeneous group, consisting of rods mainly 8–10(12) μm long and about 10–12 times as long as broad (Fig. 1e). They have no swellings, but in some cases one or two darker 'dots' are situated in either a central, subapical, or apical position. We have made no effort to distinguish between the various types of 'dotted rods' in this work. They are of little interest in *Amphigymnia* but occur in the subgenus *Cyclocheila* and subgenus *Parmelia* sections *Parmelia* and *Bicornuta.* Plain (i.e. non-'dotted') rods, on the other hand, occur in a few *Amphigymnia* species, such as *Parmelia eciliata* and *P. mesotropa.* They form a transition between weakly sublageniform and filiform conidia.

(*e*) *Filiform conidia.* Filamentous conidia have been described as filiform by, for example, Vainio (1890), Moberg (1977), and Vobis (1980). Their diameter is usually about 1 μm or less, so that the conidia are at least 15–20 times as long as broad (Fig. 1a). Plain rod-shaped conidia mainly differ from filiform conidia in being broader in relation to their length and

usually less than 10 μm long. In the Parmeliaceae longly filiform, curved conidia, about 30 μm long, are known in *Parmeliopsis*. In *Parmelia s. lat.* filiform conidia (usually less than 20 μm long) occur rarely in *Simplices* and *Cyclocheila* but are common in *Amphigymnia*. They are mainly straight, but occasionally a conidium may be bent or curved.

The shape and size of most forms of conidia were found to show very little variation within a single species. Filiform conidia were a notable exception, varying considerably in length from specimen to specimen of a species, although they were often of fairly uniform size within individual pycnidia.

Important thalline characters in the subgenus *Amphigymnia* are the presence or absence of vegetative propagules, cilia, and maculae, and the colour of the lower cortex. These characters have been discussed in detail by Hale (1965). For further comments, see below under 'Circumscription of the species' (p. 153).

A number of more or less well established species pairs were present in our area. Table 2 shows the primary species of such pairs and their sorediate and isidiate counterparts.

Table 2 Species counterparts in East African representatives of *Parmelia* subgenus *Amphigymnia*.

No soralia or isidia	Sorediate	Isidiate
P. abessinica	*P. hababiana*	
P. aldabrensis		*P. kwalensis*
P. amaniensis	*P. subarnoldii*	
P. andina	*P. austrosinensis*	
P. cetrata	*P. reticulata*	*P. subisidiosa*
P. eciliata	*P. perlata* (?)	*P. crinita*
P. erubescens	*P. subsumpta*	*P. subtinctoria*
P. euneta	*P. subschimperi*	
P. hololoba	*P. cooperi*	*P. pseudocrinita*
P. jacarandicola	*P. direagens* (?)	
P. maclayana	*P. poolii*	
P. nilgherrensis	*P. lobulascens*	
P. soyauxii	*P. defecta*	*P. stuhlmannii*
P. subcolorata	*P. permutata*	
P. taitae	*P. pseudograyana*	
P. uberrima	*P. louisianae* (?)	
P. vivida	*P. aprica*	
P. zollingeri	*P. gardneri*	

Chemistry

Atranorin and usnic acid are present either separately or jointly in the upper cortex. The β-orcinol depsidone psoromic acid is restricted to the soralia in *Parmelia direagens*, and to the cortex near the apothecia in *P. jacarandicola*. In the medulla the following substances occur: orcinol depsides (lecanoric and gyrophoric acids), orcinol depsidones (alectoronic, α-collatolic, and physodic acids, norlobaridone, loxodine, and the lividic acid complex), β-orcinol depsides (generally lacking in the species of our area except that the mainly cortical substance atranorin may be responsible for the K+ yellow reaction in the medulla of *P. praesorediosa*), β-orcinol depsidones (stictic, norstictic, salazinic, galbinic, protocetraric, fumarprotocetraric, and echinocarpic acids), fatty acids (caperatic and protolichesterinic acids, the reddenda fatty acid complex, and other unknowns), a xanthone (lichexanthone), and various pigments. The substances, with the species in which they occur, are presented in Tables 3–5. Only those of diagnostic value are listed, while substances which in our

Table 3 Chemical properties of species without soralia and isidia.

	lec	gyr	nlb	alc	liv	stc	nst	sal	pso	pc	fpc	fat	pgm	ind	atr	usn
P. abessinica	.	.	±	.	.	.	.	.	.	.	.	±	.	.	×	.
P. aldabrensis	.	.	.	.	.	×	×	.	.	.	.	.	.	.	.	.
P. amaniensis	.	.	.	±	.	.	.	.	.	×	.	±	.	.	×	.
P. andina	×	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.
P. cetrata	.	.	.	.	.	.	.	×	.	.	.	.	.	.	+	.
P. durumae	.	.	.	×	.	.	.	.	.	.	.	.	.	.	×	.
P. eciliata	.	.	.	.	.	×	.	.	.	.	.	.	.	.	×	.
P. erubescens	.	.	×	.	.	.	.	×	.	.	.	.	.	.	+	.
P. euneta	.	±	±	.	.	.	±	.	.	.	.	.	.	.	×	.
P. eurysaca	.	.	.	.	.	.	.	×	.	.	.	.	.	.	×	.
P. hanningtoniana	.	×	.	.	.	.	.	.	.	.	.	×	.	.	×	.
P. hololoba	×	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.
P. inexpectata	.	.	.	.	×	.	.	.	.	.	.	.	.	.	×	.
P. jacarandicola	.	×	.	.	.	.	.	.	+	.	.	.	.	.	×	.
P. leonis	.	.	.	.	.	.	.	.	.	.	.	×	.	.	×	.
P. maclayana	.	.	.	×	.	.	.	.	.	.	.	.	.	±	×	.
P. nilgherrensis	.	±	.	×	.	.	.	.	.	.	.	.	.	.	×	.
P. pigmentifera	.	.	.	.	.	.	.	.	.	.	.	.	×	×	×	.
P. soyauxii	×	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.
P. subcolorata	.	×	.	.	.	.	.	.	.	.	.	.	×	.	×	.
P. taitae	.	.	.	.	.	.	.	.	.	×	×	.	.	.	×	.
P. uberrima	.	.	.	×	.	.	.	.	.	.	.	.	.	.	×	.
P. vivida	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	×
P. zollingeri	.	.	.	.	.	.	.	.	.	×	.	±	.	.	×	.

Only substances of diagnostic importance are included. lec = lecanoric acid, gyr = gyrophoric acid, nlb = norlobaridone, alc = alectoronic acid (including α-collatolic acid), liv = the lividic acid complex, stc = stictic acid, nst = norstictic acid, sal = salazinic acid, pso = psoromic acid, pc = protocetraric acid, fpc = fumarprotocetraric acid, fat = fatty acids, pgm = pigments, ind = undetermined substances, atr = atranorin, usn = usnic acid. Symbols: × = constant; + = low concentrations; ± = occasionally present (accessory substance) or present in a chemical strain.

specimens always occur in conjunction with one of the main compounds, such as loxodine, oxyphysodic acid, connorstictic acid, constictic acid, unknown with alectoronic acid, and unknowns with stictic acid, are omitted from the tables.

In *P. pigmentifera* we found two undetermined main substances in the following Rf classes: in TDA 2–3 : 4, in HEF 4–5 : 6, and in TA 2–3 : 5–6. The medulla reacted PD+ ochraceous, K+ deep yellow, C−, KC+ red. The reactions with K and PD may have been caused either by the above mentioned unknowns or by an unknown medullary pigment, while the KC reaction points to the presence of one or two orcinol depsidones. Both substances gave a bright bluish white fluorescence under long-wave UV light.

Among the fatty acids of diagnostic importance is an array of substances which occur together, having Rf values intermediate between those of caperatic and protolichesterinic acids; they are referred to as the 'reddenda fatty acid complex'. The name is derived from their presence in, for example, *P. reddenda* Stirton (Krog & Swinscow, 1977). Unidentified fatty acids, usually with rather high Rf values, are accessory in some species.

In the *P. dilatata* group (including, for example, *P. affluens* and *P. progenes*) atranorin and usnic acids are produced together in considerable amounts. The proximity of other substances sometimes caused the spots indicating usnic acid to take on a dark sordid grey colour on the TLC plates. The presence of usnic acid in this species group has gone partly

Table 4 Chemical properties of species with isidia, serediate isidia, or dactyls.

	lec	gyr	nlb	alc	phy	stc	nst	sal	pc	ech	fat	pgm	lcx	ind	atr	usn
P. crinita	.	.	.	.	.	×	.	.	.	.	.	.	.	.	×	.
P. cryptoxantha	.	.	.	.	.	.	.	.	.	×	×	×	.	.	×	.
P. kwalensis	.	.	.	.	.	×	×	.	.	.	.	.	.	.	×	.
P. lophogena	.	×	.	.	.	.	.	.	.	.	×	.	.	.	×	.
P. mellissii	.	.	.	×	.	.	.	.	.	.	.	.	.	.	×	.
P. planatilobata	.	×	.	.	.	.	.	.	.	.	.	.	.	.	×	.
P. pseudocrinita	.	×	.	.	.	.	.	.	.	.	.	.	.	.	×	.
P. stuhlmannii	×	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.
P. subisidiosa	.	.	.	.	.	.	.	×	.	.	.	.	.	.	+	.
P. subtinctoria	.	.	×	.	.	.	.	×	.	.	.	.	.	.	+	.
P. sulphurata	.	.	.	.	.	.	.	.	.	.	.	×	.	.	+	.
P. tinctorum	×	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.
P. tsavoensis	.	.	.	.	×	.	.	.	.	.	.	.	.	.	×	.
P. ultralucens	.	.	.	.	.	.	.	×	.	.	.	.	×	.	×	.
P. xanthina	.	.	.	.	.	.	.	.	.	.	×	.	.	×	.	×

Only substances of diagnostic importance are included. lec = lecanoric acid, gyr = gyrophoric acid, nlb = norlobaridone, alc = alectoronic acid (including α-collatolic acid), phy = physodic acid, stc = stictic acid, nst = norstictic acid, sal = salazinic acid, pc = protocetraric acid, ech = echinocarpic acid, fat = fatty acids, pgm = pigments (including vulpinic acid), lcx = lichexanthone, ind = undetermined substances, atr = atranorin, usn = usnic acid. Symbols: × = constant; + = low concentrations.

unnoticed, and the grey spots were thought by Hale (1971*c*, 1977), for instance, to represent an unknown substance.

Usually the chemical properties of lichens remain unchanged after extended storage in the herbarium. However, we noticed that in old specimens with alectoronic and α-collatolic acids we often obtained additional spots below those of the main substances on the TLC plates, correlated with an ochraceous reaction with C in the medulla. They were especially prevalent in the *P. nilgherrensis* group, of which many old collections exist. We found no correlation between morphological characters and the presence or absence of such substances, and are inclined to regard them as artefacts. On the other hand, an unknown with low Rf values, occurring with alectoronic acid in a chemical strain of *P. maclayana,* appears to be of diagnostic value. It will be referred to below as 'unknown with alectoronic acid'.

The African chemotype of *P. xanthina* contained an undetermined C−, KC+ red substance which is probably close to gyrophoric acid. It ran slightly higher than gyrophoric acid on the TLC plates in TDA and HEF.

Ecology and distribution

Tropical East Africa offers a wide range of habitats, from the sea coast to more than 5000 m altitude, and from subdeserts and savannas to montane rain forests. Very few lichens are found in the large subdesert areas of northern Kenya and Uganda and southern Ethiopia, and also in the dry thornbush savannas which lie below 1000 m altitude and have an annual rainfall of less than 500 mm.

While species of *Parmelia* subgenus *Hypotrachyna* are absent from the East African sea coast and lowlands below *c.* 800 m altitude (Krog & Swinscow, 1979), the subgenus *Amphigymnia* is represented there by more than a dozen species. They grow partly in mangroves at sea level and partly in the coastal forest and low coastal hills up to *c.* 500 m. All are drought tolerant, and several of them are found also in the upland savannas. The coastal

Table 5 Chemical properties of species with soralia.

	lec	gyr	nlb	alc	stc	nst	sal	pso	glb	pc	fpc	ech	fat	pgm	atr	usn
P. aprica	.	.	.	.	.	.	.	.	.	×	.	.	±	.	.	×
P. araucariarum	.	.	.	.	.	.	.	.	.	.	.	.	×	×	×	.
P. austrosinensis	×	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.
P. bangii	.	.	.	.	×	.	.	.	.	.	.	.	.	.	×	.
P. cooperi	×	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.
P. cristifera	.	.	.	.	.	.	×	.	.	.	.	.	.	.	×	.
P. defecta	×	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.
P. dilatata	.	.	.	.	.	.	.	.	.	×	.	×	.	×	×	×
P. direagens	.	±	.	±	.	.	.	×	.	.	.	.	.	.	×	.
P. gardneri	.	.	.	.	.	.	.	.	.	×	.	.	±	.	×	.
P. grayana	.	.	.	.	.	.	.	.	.	.	.	.	×	.	×	.
P. hababiana	.	.	±	.	.	.	.	.	.	.	.	.	±	.	×	.
P. indoafra	.	×	×	.	.	.	.	.	.	.	.	.	.	.	×	.
P. lobulascens	.	±	.	×	.	.	.	.	.	.	.	.	.	.	×	.
P. louisianae	.	.	.	×	.	.	.	.	.	.	.	.	.	.	×	.
P. parahypotropa	.	.	.	.	.	×	×	.	×	.	.	.	±	.	×	.
P. pardii	.	.	.	.	.	.	.	.	.	×	×	.	.	.	×	.
P. perlata	.	.	.	.	×	.	.	.	.	.	.	.	.	.	×	.
P. permutata	.	×	.	.	.	.	.	.	.	.	.	.	.	×	×	.
P. pilosa	.	.	.	.	.	.	.	.	.	.	.	.	×	.	×	.
P. poolii	.	.	.	×	.	.	.	.	.	.	.	.	.	.	×	.
P. praesorediosa	.	.	.	.	.	.	.	.	.	.	.	.	×	.	×	.
P. pseudograyana	.	.	.	.	.	.	.	.	.	×	×	.	.	.	×	.
P. rava	.	.	.	.	.	.	.	.	.	×	.	.	±	.	×	×
P. reticulata	.	.	.	.	.	.	±	.	.	.	.	.	±	.	+	.
P. rimulosa	.	.	.	×	.	.	.	.	.	.	.	.	.	.	×	.
P. sancti-angelii	.	×	.	.	.	.	.	.	.	.	.	.	.	.	×	.
P. subarnoldii	.	.	.	±	.	.	.	.	.	×	.	.	±	.	×	.
P. subschimperi	.	±	±	.	.	±	.	.	.	.	.	.	.	.	×	.
P. subsumpta	.	.	±	.	.	.	±	.	.	.	.	.	.	.	+	.
P. umbrosa	.	×	.	.	.	.	.	.	.	×	.	.	.	.	×	.

Only substances of diagnostic importance are included. lec = lecanoric acid, gyr = gyrophoric acid, nlb = norlobaridone, alc = alectoronic acid (including α-collatolic acid), stc = stictic acid, nst = norstictic acid, sal = salazinic acid, pso = psoromic acid, glb = galbinic acid, pc = protocetraric acid, fpc = fumarprotocetraric acid, ech = echinocarpic acid, fat = fatty acids, pgm = pigments, atr = atranorin, usn = usnic acid. Symbols: × = constant; + = low concentrations; ± = occasionally present (accessory substance) or present in a chemical strain.

Table 6 Coastal species of *Parmelia* subgenus *Amphigymnia* in East Africa, arranged by the lowest altitude at which they occur, and showing the altitudinal range in metres.

P. kwalensis	0	*P. gardneri*	0–2000
P. pigmentifera	0–70	*P. uberrima*	0–2000
P. parahypotropa	0–300	*P. tinctorum*	0–2700
P. aldabrensis	0–1000	*P. reticulata*	0–3000
P. zollingeri	0–1000	*P. dilatata*	300–900
P. durumae	0–1100	*P. cristifera*	300–1450
P. hololoba	0–1800	*P. sulphurata*	480

Table 7 Photophilous, drought tolerant inland species of *Parmelia* subgenus *Amphigymnia* in East Africa, arranged by the lowest altitude at which they occur, and showing the altitudinal range in metres. See Table 6 for additional species.

P. leonis	700–1400	*P. grayana*	1160–1500
P. praesorediosa	700–1800	*P. rava*	1250–1800
P. hababiana	800–2650	*P. pilosa*	1300–2000
P. andina	900–2400	*P. subtinctoria*	1300–2300
P. maclayana	900–2200	*P. pseudograyana*	1400–1900
P. poolii	900–2300	*P. indoafra*	1450–2600
P. abessinica	900–2600	*P. xanthina*	1500
P. vivida	920	*P. stuhlmannii*	1500–2100
P. aprica	1000	*P. cooperi*	1500–3000
P. louisianae	1000	*P. pardii*	1650–1750
P. tsavoensis	1000	*P. hanningtoniana*	1700
P. soyauxii	1000–2100	*P. defecta*	1750–2100
P. sancti-angelii	1000–2800	*P. jacarandicola*	1900
P. austrosinensis	1000–3000	*P. taitae*	1980–2050

species, with their altitudinal ranges, are shown in Table 6; they include, for example, the widespread, photophilous *P. tinctorum* and the ubiquitous *P. reticulata*.

Drought tolerant photophilous species which do not reach the coast are found in savannas, bushed grassland, well lit sites in the montane forests, and artificial habitats such as parks, plantations, town avenues, and roadside trees and gardens (Table 7).

Species with a somewhat higher moisture requirement are found in the more shaded sites in the lower montane forests and those parts of the inselbergs which are regularly influenced by mist. They often grow together with savanna species, but are here included among those of the montane forests when they are largely absent from drier habitats. Species that are more exacting in their moisture requirements are often best developed in the upper montane forest where the rainfall is higher and more equally distributed throughout the year, especially on the wetter slopes of the mountains. In the lower part of the alpine zone, above *c.* 3500 m, there is still ample moisture, combined with high light intensity and low night temperatures. Only four of our species, *P. euneta*, *P. lobulascens*, *P. nilgherrensis*, and *P. subschimperi*, extend through the ericaceous zone and into the low alpine zone.

Table 8 Montane and low alpine species of *Parmelia* subgenus *Amphigymnia* in East Africa, arranged by the lowest altitude at which they occur, and showing the altitudinal range in metres. *Parmelia reticulata* is an additional species, included in Table 6.

P. subarnoldii	500–3000	*P. crinita*	1400–3400
P. pseudocrinita	700–2600	*P. direagens*	1500–2600
P. planatilobata	800–1000	*P. bangii*	1500–3200
P. amaniensis	800–1150	*P. cryptoxantha*	1550–2100
P. eciliata	800–1200	*P. euneta*	1600–3750
P. ultralucens	900	*P. subcolorata*	1700–2500
P. inexpectata	1100	*P. rimulosa*	1800–2900
P. permutata	1100–2400	*P. subisidiosa*	1800–3200
P. umbrosa	1300–2100	*P. lobulascens*	1800–3600
P. erubescens	1400	*P. subschimperi*	1800–3600
P. subsumpta	1400–2100	*P. araucariarum*	2000–2100
P. lophogena	1400–2400	*P. mellissii*	2000–2400
P. cetrata	1400–2600	*P. nilgherrensis*	2000–3600
P. perlata	1400–3100		

Table 9 Species of *Parmelia* subgenus *Amphigymnia* which are not known outside Africa.

P. aldabrensis	*P. kwalensis*	*P. stuhlmannii*
P. amaniensis	*P. leonis*	*P. subcolorata*
P. aprica	*P. lophogena*	*P. subschimperi*
P. cryptoxantha	*P. pardii*	*P. taitae*
P. defecta	*P. pigmentifera*	*P. tsavoensis*
P. durumae	*P. pseudograyana*	*P. uberrima*
P. hololoba	*P. rava*	*P. umbrosa*
P. inexpectata	*P. rimulosa*	*P. vivida*
P. jacarandicola	*P. soyauxii*	

The species of the montane forests and the lower part of the alpine zone are shown in Table 8. (In addition comes *P. reticulata*, included in Table 6 as one of the species that reach the coast.) The subgenus *Amphigymnia* is not represented in the upper parts of the alpine zone, above *c.* 4000 m altitude.

Of the 70 *Amphigymnia* species here recorded for East Africa, 26 species, or nearly 40 per cent, are not yet known outside Africa (Table 9). Among the remaining species, 35 are found also in the Americas; some of them are so far known only from Africa and the Americas, namely *Parmelia abessinica*, *P. araucariarum*, *P. bangii*, ?*P. eurysaca*, *P. hanningtoniana*, ?*P. louisianae*, *P. pilosa*, and *P. subsumpta.* Thirty-three are known from Asia, and of these species the following are known only from Africa and Asia: *Parmelia cooperi*, *P. direagens*, ?*P. euneta*, *P. indoafra*, *P. lobulascens*, *P. nilgherrensis*, *P. planatilobata*, and *P. pseudocrinita.* Twenty-three of the East African species occur in the Australian region; they are all known also from other regions. Only five cosmopolitan, mainly temperate species are common to East Africa and Europe; they are *P. austrosinensis*, *P. cetrata*, *P. crinita*, *P. perlata*, and *P. reticulata.*

Discussion

Circumscription of the species

In his world monograph Hale (1965) discussed the relative taxonomic value of various morphological and chemical characters on the basis of their degree of association with each other. He found that cilia had a positive or negative correlation with more than half of the characters considered, and deduced that they were of importance at species level. Similarly, maculae, a white marginal zone on the under side, an entirely brown under side, and a perforated apothecial disc were found to be valid characters, whereas spore size and ornamentation of the thalline exciple were not. Conidia were assumed to have no importance and were not investigated. Chemical strains were accepted in a limited way; many of them have been regarded as species in subsequent publications by the same author. It should be borne in mind that Hale's monograph appeared before the advent of TLC, so that knowledge of the chemical properties of the species was then in many cases inferior to that reached during the last decade.

We have had the advantage of studying the East African Amphigymnias in the field and of collecting numerous specimens of the commoner species from sites with differing ecology. This has enabled us to evaluate the morphological variation within the species in the light of environmental factors, and to form an opinion on the relative taxonomic value of the various characters as expressed in the species of our area. As might be expected, we have observed that species with a great ecological amplitude usually show a much greater morphological variation than species with a limited range. In a moist, shady habitat in an area with favourable temperatures the thallus is often membranaceous, greenish in colour, has long, slender

cilia and distinct maculae, whereas plants growing in a well lit site, subjected to drought or low temperatures conducive to slow growth, in general have a coriaceous thallus, a grey colour more or less tinged with brown, short, stunted and coarse cilia, and less conspicuous maculae. At their extremes such plants look very different and have often been interpreted as distinct species.

Taking the environmentally induced variation into account, we find that most of the characters listed by Hale (1965) are of value at species level, but with certain reservations. A normally ciliate species, such as *Parmelia nilgherrensis*, may rarely lack cilia, while a few normally eciliate species, such as *P. cristifera* and *P. gardneri*, may produce rudimentary cilia in the lobe axils. A strongly maculate species clearly differs from a species in which maculae are always indistinct or absent, but in a normally maculate species it is possible for saxicolous specimens with a coriaceous thallus to develop very few maculate areas. Presence or absence of a perforated apothecial disc is fairly constant in most species but varies greatly in some. In *P. euneta* and *P. maclayana*, for example, the apothecia may all be perforate, or all imperforate, or both types may be present on a single specimen, so that the character is of limited diagnostic value in these two species. A white marginal zone on the under side is characteristic of some species, such as *P. leonis* and *P. uberrima*, but occurs only in some specimens of, for example, *P. abessinica* and *P. andina*. In the *P. erubescens* species complex, as here delimited, the colour of the under side varies from black through brown to ivory.

The various types of vegetative propagules are usually considered to be species specific, but in some species there is a complete intergradation between granular soredia, sorediate isidia, non-sorediate isidia, and dactyls. This is the case in, for example, *P. lophogena* and *P. mellissii*. We have also found that *P. tinctorum* is subject to variation in its vegetative propagules, which range from simple or branched, slender, cylindrical isidia to coarse, branched isidia and closed or open dactyls. Both isidia and dactyls may at times disintegrate partly or wholly into granular soredia. We have chosen to regard *P. pseudotinctorum* (coarse isidia and dactyls) as conspecific with *P. tinctorum* (slender isidia), since the variation is largely continuous and both morphotypes have the same type of spores and conidia, and mainly the same ecological requirements. If a distinction were to be maintained, we believe that it should be at infraspecific level.

We do not agree with Hale (1965) that spore size alone is not a valid character. In our experience there is little variation in spore length within species whose spores are below 20 μm long, so that two subgroups whose spores are respectively above and below about 16 μm can be recognized (Table 1). In species with medium sized spores, on the other hand, the spores may vary between 20 and 30 μm, often with a maximum around 22–25 μm, while in those with large spores, the spores may in extreme cases show variation between 25 and 40 μm, usually with a maximum around 28--30 μm. There is in our area a clear discontinuity between species with small spores and those with large spores, and we regard this character as species specific.

There is at present no common agreement on the function of the lichen conidia. A sexual function for them has not been conclusively proved, but nor has their asexual nature been firmly established. Regardless of their function, their constancy within morphologically well delimited species and partly also within supraspecific units show that a taxonomic value should be assigned to them that would normally not be bestowed upon vegetative propagules. In agreement with, for example, Henssen & Jahns (1973) we consider the shape of the conidia to be species specific, and like Moberg (1977) we believe that they are of taxonomic significance also at the supraspecific level.

In *Amphigymnia* we have noted a strong correlation between imperforate apothecia and sublageniform conidia on the one hand and perforate apothecia and filiform conidia on the other, although there are exceptions to this rule (Table 10). *Parmelia abessinica*, for example, has perforate apothecia but weakly sublageniform conidia. In *P. maclayana*, in which the apothecia may be perforate or not, the conidia are sublageniform, whereas in *P. euneta*, with similarly variable apothecia, they are filiform.

Table 10 Number of species with either filiform or sublageniform conidia, arranged by presence or absence of perforate apothecial discs.

	Conidia	
Apothecia	filiform	sublageniform
perforate	24	4
imperforate	1	13

Table 11 Epithets applied to various chemotypes in the *Parmelia euneta—Parmelia subschimperi* species pair.

Substances	No soralia or isidia	Soralia
gyrophoric acid	*euneta* (1877–78)	*neolobulascens* (1975)
gyrophoric acid norstictic acid	*composita* (1972)	*subcompositum* (1977)
gyrophoric acid norlobaridone norstictic acid (±)	unnamed	*balensis* (1975)
norlobaridone	unnamed	*subschimperi* (1972)
norlobaridone norstictic acid	*spilota* (1973)	unnamed
norstictic acid	unnamed	—

In the delimitation of the species we assign greater taxonomic value to characters of spores and conidia than we do to characters of the thallus. Many secondary species without apothecia still produce pycnidia, and if conidia can be found they offer a valuable guide to the correct interpretation of the species.

Chemical characters show no continuous variation, with the exception of accessory substances which vary from abundance to absence within a given species and are commonly regarded as of no taxonomic value. All other cases of chemical variation represent easily registered discontinuities, and have therefore been regarded as species specific by some authors. However, as with the morphological variation we have attempted to evaluate each case of chemical variation individually on the basis of trends observed in our material.

Winnem (1975) clarified the chemical properties of the sorediate species *P. direagens.* She found that it had three chemical strains: (1) psoromic acid, gyrophoric acid, and alectoronic acid; (2) psoromic acid and gyrophoric acid; and (3) psoromic acid and alectoronic acid. The psoromic acid, an extremely rare substance in *Amphigymnia,* is mainly connected with the soralia in *P. direagens*, which is an unusual situation in *Parmelia* but known in certain other genera, for example *Usnea* (Swinscow & Krog, 1979). In our opinion the presence of this common denominator unites the morphologically uniform chemotypes and shows beyond doubt that they merely represent chemical strains within a species. Apart from the presence of psoromic acid, a depside and a depsidone of the orcinol series occur separately or jointly.

A parallel to this example is found in the chemical variation of the *P. euneta—P. subschimperi* species pair, although there is no common denominator present (Table 11).

The species comprise strongly maculate, ciliate plants with intermediate spores, filiform conidia, and a montane to low alpine distribution. Winnem (1975) showed that norstictic acid was accessory in this group and of no taxonomic importance. The remaining substances, gyrophoric acid and norlobaridone, may occur separately or jointly. As in *P. direagens* this is also a situation involving a depside and a depsidone of the orcinol series.

The *P. amaniensis—P. subarnoldii* pair are ciliate, emaculate species with imperforate apothecia, a strongly dentate-ciliate thalline margin, large, thick-walled spores, and sublageniform conidia. The following chemical strains occur in each species: (1) protocetraric acid and alectoronic acid; (2) protocetraric acid and α-collatolic acid, $\pm$ alectoronic acid; and (3) protocetraric acid and protolichesterinic acid (Table 12). Spores, conidia, and thallus morphology afford several valid characters by which to define this species pair, and chemically protocetraric acid is a common denominator. We have here a substitution situation involving two closely related orcinol depsidones and a fatty acid.

Another example involving an orcinol depsidone and a fatty acid is that of the *P. abessinica—P. hababiana* species pair, each of which is known in the following chemical strains: (1) norlobaridone; (2) norlobaridone and protolichesterinic acid; and (3) protolichesterinic acid.

A group of mainly Australian and South American species poses problems related to variation in both cortical and medullary substances. All specimens have imperforate or narrowly perforate apothecia, small spores, and a distinctly maculate upper side. The underside varies from black in the centre with a broad, brown or mottled marginal zone through uniformly brown to ivory. The rhizines are usually dimorphous, and rhizines and papillae often, but not always, reach the lobe margins. The majority of species have negligible quantities of atranorin in the cortex, often in too small amounts to be detected with TLC, but

Table 12 Epithets applied to various chemotypes in the *Parmelia amaniensis—Parmelia subarnoldii* species pair.

Substances	No soralia or isidia	Soralia
protocetraric acid alectoronic acid	*amaniensis* (1926)	*deflectens* (1979)
protocetraric acid α-collatolic acid	*pachyspora* (1965)	unnamed
protocetraric acid protolichesterinic acid	unnamed	*subarnoldii* (1961)

Table 13 The oldest epithets for the various chemotypes in the *Parmelia erubescens* species complex.

Substances	No soralia or isidia	Sorediate	Isidiate
salazinic acid	*erubescens* (1877–78)	*subsumpta* (1869)	unnamed
norlobaridone	*recipienda* (1885)	*conferendum* (1977)	*haitiensis* (1959)
salazinic acid norlobaridone	unnamed	*reitzii* (1977)	*subtinctoria* (1930)

some Central and South American species, such as *P. subcaperata* Krempelh. and *Parmotrema neotropicum* Kurok., have copious amounts of usnic acid together with medium amounts of atranorin. In the Parmeliaceae there is no precedent for accepting such large variation in cortical substances within a species. The presence of usnic acid in the cortex is here correlated with salazinic acid in the medulla, while species with only traces of atranorin in the cortex may produce salazinic acid and norlobaridone separately or jointly. That the variation in cortical substances does not parallel that of the medulla is a further reason for regarding the species that produce usnic acid as distinct from those with only traces of atranorin (referred to below as the *P. erubescens* complex).

The oldest epithets available for each chemotype within the *P. erubescens* species complex are listed in Table 13, providing an example of chemical variation involving an orcinol depsidone and a β-orcinol depsidone. As in the examples mentioned above we believe that these chemotypes also should be regarded as chemical strains. However, since the relevant primary species are poorly represented in our area, they are in need of further study, especially with regard to their conidial characters, in order to ascertain their relationship with each other. We have therefore chosen to treat the chemotypes occurring in our area as chemical strains, but do not formally reduce the extra-African chemotypes to synonymy at this point.

When the chemical relationship seemed more complicated than in the examples given above, or we felt that we had studied insufficient material, we have hesitated to apply the theory of chemical strains until further evidence can be produced. Some examples follow.

The morphological differences between the two species pairs *P. euneta—P. subschimperi* and *P. nilgherrensis—P. lobulascens* are few and insignificant; they are mainly that the *P. nilgherrensis* pair has a higher frequency of perforate apothecia and on the whole a more coriaceous thallus and more irregularly incised lobes. However, the two species pairs differ both in basic chemistry (gyrophoric acid and norlobaridone versus alectoronic acid) and in accessory substances (norstictic acid versus gyrophoric acid), while we have not yet come upon specimens with a combination of the two orcinol depsidones alectoronic acid and norlobaridone. In view of these considerable chemical differences, which are correlated with a few weak morphological traits, we regard the two species pairs as distinct from each other.

Parmelia inexpectata differs from *P. amaniensis* in that it lacks protocetraric acid (the common denominator in the *P. amaniensis* complex), while it produces an array of orcinol depsidones (lividic acid and associated substances), none of which occur in *P. amaniensis*. Since *P. inexpectata* is known from very few collections, we feel that we have insufficient grounds for including the species in *P. amaniensis* for the time being, especially since it differs in several chemical characters.

The two sorediate species *P. grayana* (protolichesterinic acid) and *P. pseudograyana* (fumarprotocetraric and protocetraric acids) are morphologically virtually indistinguishable. The supposed parent morph of *P. pseudograyana*, *P. taitae*, is known only with the β-orcinol depsidones. This species pair appears to be restricted to Africa, while *P. grayana* is widely distributed. We should like to see much more material of *P. taitae*, and preferably also fruit bodies in *P. pseudograyana*, before we make a final decision on the relationship between the two secondary species.

It is difficult to assess the relationship between chemically discordant secondary species when the corresponding primary species are not known. In such cases it is preferable to regard the species as distinct until further evidence becomes available.

The underlying causes of chemical diversity in lichens are not known. Theoretically, a single mutation influencing the biogenetic pathway at an early point may change the chemical end product considerably. If sexual reproduction is assumed to take place among lichens, cross fertilization between two individuals with different chemical properties might result in the spores from one apothecium giving rise to plants of different chemotypes. If one further assumes that some gene exchange takes place, a new chemotype characterized by a combination of substances may result. Chemotypes originating in that manner would probably not be regarded as distinct species.

It is possible that conidia rarely function as spermatia in lichens, or, if they do, that fertilization usually takes place between conidia and ascogones produced on the same thallus. However, if cross fertilization does occur under certain circumstances, the conditions in the tropical rain-forests would be conducive to it. There the various lichens are crowded and often multilayered on tree trunks and branches, and they are subjected almost daily to tropical showers and water condensed from heavy mist, which could carry conidia from one plant to another with minimal risk of desiccation.

Generic concept and infrageneric classification

Genus *Parmelia s. lat.* has in recent years been divided into a number of genera. As we have stated earlier (Krog & Swinscow, 1979), we believe some of these genera to be based on characters of little importance at the generic level, the result being obscure delimitation between some neighbouring genera. We have therefore been reluctant to accept the new genera proposed, although we believe that a satisfactory division of *Parmelia s. lat.* into several genera will eventually be reached.

According to Hale's main division of *Parmelia s. lat.*, *Parmelia s. str.* has a paraplectenchymatous upper cortex and a non-pored epicortex frequently bearing pseudocyphellae, while the other segregates possess a palisade plectenchymatous upper cortex and a pored epicortex without pseudocyphellae (Hale, 1976*a*). We agree in this major division, but have not yet reached a decision on the interpretation of the residual genera in *Parmelia s. lat.* Although the generic name *Parmotrema* primarily applies to the group of lichens that are dealt with here, we hesitate to adopt it until the genus has been satisfactorily circumscribed, notably in relation to *Parmelia* subgenus *Cyclocheila sensu* Krog & Swinscow (1979). The conidia may prove to be of considerable value in the circumscription of the parmelioid genera.

For a subdivision of *Amphigymnia,* various characters have been employed. Vainio (1890) relied on the colour of the upper cortex (presence or absence of usnic acid) when he proposed the subsections *Subflavescens* Vainio and *Subglaucescens* Vainio. Gyelnik (1932) regarded Vainio's subsections as sections and further subdivided them into each two subsections (*Eciliatae—Ciliatae*, *Eciliolae—Ornaticolae*) on the basis of presence or absence of cilia.

Hale (1965) found that the presence or absence of cilia was a character of greater importance at section level than the colour of the upper cortex. He proposed the following scheme:

- Sect. *Amphigymnia* [lobe margins eciliate or rarely with sparse cilia in the axils].
- Sect. *Subflavescentes* (Vainio) Gyelnik [margins and apices of lobes distinctly ciliate].
  - Subsect. *Subflavescentes* [upper cortex emaculate].
    - Ser. *Subflavescentes* [usnic acid present].
    - Ser. *Emaculatae* Hale [usnic acid absent].
  - Subsect. *Ornaticolae* Gyelnik [upper cortex maculate].
    - Ser. *Subpallidae* Hale [under side brown, rhizinate to the margins].
    - Ser. *Ornaticolae* [under side black in the centre, with a commonly white or mottled, naked marginal zone].

We are undecided whether to regard the presence of cilia as a valid character for infrageneric classification in *Amphigymnia,* since its correlation with other characters is not yet clear. In ser. *Subpallidae* there appears to be correlation between a strongly maculate upper cortex, rhizine morphology, and chemical traits, whilst in most other cases the presence of maculae seems uncorrelated with other characters. We find the presence or absence of usnic acid in the cortex to be of no taxonomic value above species level. However, a classification of the amphigymnioid species can only be settled on the basis of a world wide study. Before that is possible, the delimitation of the genus *Parmotrema* must be conclusively agreed upon.

The East African *Amphigymnia* species

Key to the species

1a Soralia and isidia absent . . . . 2 (p. 159)
1b Soralia or isidia present 46

46a Isidia (including sorediate isidia and dactyls) present . . . . 47 (p. 161)
46b Isidia absent. Soralia present . . . . 62 (p. 162)

Soralia and isidia absent

2a (1a) Marginal cilia absent 3
2b Marginal cilia present 6

3a (2a) Thallus yellow (usnic acid present) . . . . **68. P. vivida** (p. 223)
3b Thallus grey (usnic acid absent) 4

4a (3b) Apothecia imperforate. Medulla C−, PD+ orange-red (protocetraric acid) **70. P. zollingeri** (p. 225)
4b Apothecia perforate. Medulla C+ red, PD− (lecanoric acid) 5

5a (4b) Plant saxicolous, strongly attached. Lobes less than 1 cm broad **53. P. soyauxii** (p. 210)
5b Plant normally corticolous, loosely attached. Lobes more than 1 cm broad **4. P. andina** (p. 168)

6a (2b) Medulla pigmented pale yellow, ochraceous, or salmon pink, pigment K− 7
6b Medulla white, at most with patches of an ochraceous, K+ purple pigment near the lower cortex 8

7a (6a) Apothecia imperforate, with a dentate-ciliate thalline margin. Medulla UV+ (undetermined substances). Coastal species . . . . . **42. P. pigmentifera** (p. 201)
7b Apothecia perforate, with a smooth, eciliate thalline margin. Medulla UV− (gyrophoric acid). Upland species . . . . **56. P. subcolorata** (p. 213)

8a (6b) Upper cortex with a reticulate pattern of maculae and cracks. Rhizines in part squarrose. Salazinic acid present . . . . **9. P. cetrata** (p. 172)
8b Upper cortex without a reticulate pattern of maculae and cracks. Rhizines not squarrose. Salazinic acid present or absent 9

9a (8b) Underside with a distinct, white marginal zone 10
9b Underside with a brown or mottled marginal zone 14

10a (9a) Apothecia perforate. Medulla UV− 11
10b Apothecia mainly imperforate. Medulla UV+ 13

11a (10a) Underside almost entirely white. Medulla C−, KC− (protolichesterinic acid) **31. P. leonis** (p. 191)
11b Underside black in the centre, white peripherally. Medulla C+ or C−, KC+ or KC− . 12

12a (11b) Lobe margins flat or revolute. Medulla C+ red (lecanoric acid) **26. P. hololoba** (p. 186)
12b Lobe margins ascending. Medulla C− (norlobaridone and/or protolichesterinic acid) **1. P. abessinica** (p. 165)

13a (10b) Spores less than 20 μm long. Only alectoronic acid present **65. P. uberrima** (p. 220)
13b Spores more than 20 μm long. Both alectoronic and α-collatolic acids present **17. P. durumae** (p. 178)

14a (9b) Apothecia present 15
14b Apothecia absent 30

15a (14a) Spores more than 20 μm long 16
15b Spores less than 20 μm long 21

16a (15a) Upper cortex emaculate. Apothecia imperforate 17
16b Upper cortex distinctly maculate. Apothecia perforate or imperforate 20

17a (16a) Apothecia with an even, eciliate thalline margin. Stictic acid present **18. P. eciliata** (p. 180)
17b Apothecia normally with a dentate-lobulate and/or ciliate thalline margin. Stictic acid absent 18

18a (17b) Spores 22–26 μm long. Alectoronic and α-collatolic acids present **17. P. durumae** (p. 178)
18b Spores 25–28 (40) μm long. Chemistry various 19

19a (18b) Medulla with substances in the lividic acid complex . . . **28. P inexpectata** (p. 188)
19b Medulla with protocetraric acid (usually in combination with alectoronic, α-collatolic, or protolichesterinic acid) . . . . **3. P. amaniensis** (p. 167)

20a (16b) Medulla UV+ (alectoronic acid, $\pm$ α-collatolic acid, $\pm$ gyrophoric acid) **37. P. nilgherrensis** (p. 197)
20b Medulla UV– (gyrophoric acid and/or norlobaridone, $\pm$ norstictic acid) **20. P. euneta** (p. 181)

21a (15b) Upper cortex distinctly maculate 22
21b Upper cortex emaculate or faintly maculate 25

22a (21a) Thalline exciple with coarse, isidioid protuberances. Medulla C+ rose, PD– (gyrophoric acid) . . . . **25. P. hanningtoniana** (p. 185)
22b Thalline exciple smooth to rugose, without isidioid protuberances. Medulla C–, PD+ or PD– 23

23a (22b) Rhizines dimorphous. Salazinic acid and norlobaridone present **19. P. erubescens** (p. 180)
23b Rhizines uniform. Chemical properties otherwise 24

24a (23b) Underside brown. Medulla PD+ orange (stictic and norstictic acids). Coast and lowland species . . . . **2. P. aldabrensis** (p. 166)
24b Underside black in the centre, white, mottled, or brown peripherally. Medulla PD– (norlobaridone and/or protolichesterinic acid). Upland species **1. P. abessinica** (p. 165)

25a (21b) Cortex PD+ sulphur yellow near the apothecia (psoromic acid present). Medulla C+ rose (gyrophoric acid) . . . . **29. P. jacarandicola** (p. 190)
25b Cortex at most PD+ pale yellow (psoromic acid absent). Medulla C+ or C– 26

26a (25b) Medulla UV+ (alectoronic acid) . . . . . . **35. P. maclayana** (p. 195)
26b Medulla UV– (alectoronic acid absent) 27

27a (26b) Plant saxicolous. Apothecia imperforate. Medulla PD+ orange-red (fumarprotocetraric acid) . . . . **62. P. taitae** (p. 217)
27b Plant normally corticolous. Apothecia perforate. Medulla PD+ or PD– (fumarprotocetraric acid absent) 28

28a (27b) Central lobes laciniate. Medulla PD+ orange (salazinic acid) **21. P. eurysaca** (p. 182)
28b Central lobes not laciniate. Medulla PD– 29

29a (28b) Lobe margins flat or revolute. Medulla C+ red (lecanoric acid) **26. P. hololoba** (p. 186)
29b Lobe margins ascending. Medulla C– (norlobaridone and/or protolichesterinic acid) (norlobaridone and/or protolichesterinic acid). Upland species **1. P. abessinica** (p. 165)

30a (14b) Medulla PD+ orange or red 31

30b	Medulla PD− (but cortex may be PD+ sulphur yellow, see 42b)	37
31a	(30a) Plant saxicolous. Fumarprotocetraric acid present	**62. P. taitae** (p. 217)
31b	Plant normally corticolous. Fumarprotocetraric acid absent	32
32a	(31b) Upper cortex distinctly maculate	33
32b	Upper cortex emaculate or faintly maculate	35
33a	(32a) Salazinic acid and norlobaridone present	**19. P. erubescens** (p. 180)
33b	Salazinic acid absent, norlobaridone present or absent	34
34a	(33b) Montane forest species. Norstictic acid present in combination with gyrophoric acid and/or norlobaridone	**20. P. euneta** (p. 181)
34b	Coastal species. Norstictic acid present in combination with stictic acid	**2. P. aldabrensis** (p. 166)
35a	(32b) Protocetraric acid present (usually in combination with alectoronic, α-collatolic, or protolichesterinic acid)	**3. P. amaniensis** (p. 167)
35b	Protocetraric acid absent	36
36a	(35b) Salazinic acid present	**21. P. eurysaca** (p. 182)
36b	Stictic acid present	**18. P. eciliata** (p. 180)
37a	(30b) Upper cortex distinctly maculate	38
37b	Upper cortex emaculate or faintly maculate	41
38a	(37a) Species of dry, well lit upland habitats	39
38b	Species of the montane forests and the alpine zone	40
39a	(38a) Medulla C+ rose (gyrophoric acid)	**25. P. hanningtoniana** (p. 185)
39b	Medulla C− (norlobaridone and/or protolichesterinic acid)	**1. P. abessinica** (p. 165)
40a	(38b) Medulla UV+ (alectoronic acid, $\pm$ α-collatolic acid, $\pm$ gyrophoric acid)	**37. P. nilgherrensis** (p. 197)
40b	Medulla UV− (gyrophoric acid and/or norlobaridone)	**20. P. euneta** (p. 181)
41a	(37b) Medulla C+ rose or red	42
41b	Medulla C−	43
42a	(41a) Lecanoric acid present	**26. P. hololoba** (p. 186)
42b	Gyrophoric acid present (combined with psoromic acid in the cortex of some lobes)	**29. P. jacarandicola** (p. 190)
43a	(41b) Substances in the lividic acid complex present	**28. P. inexpectata** (p. 188)
43b	Substances in the lividic acid complex absent	44
44a	(43b) Medulla UV− (norlobaridone and/or protolichesterinic acid)	**1. P. abessinica** (p. 165)
44b	Medulla UV+ (alectoronic acid, $\pm$ α-collatolic acid)	45
45a	(44b) Plant corticolous or saxicolous. Upland species above *c.* 1000 m altitude	**35. P. maclayana** (p. 195)
45b	Plant corticolous. Coastal and lowland species below *c.* 1000 m altitude	**17. P. durumae** (p. 178)
46a	(1b) Isidia (including sorediate isidia) or dactyls present	47
46b	Isidia and dactyls absent. Soralia present	62

Isidia (including sorediate isidia and dactyls) present

47a	(46a) Marginal cilia absent	48

47b Marginal cilia present 51

48a (47a) Medulla PD+ orange-red (protocetraric acid) . . . . . . **71. P. sp. A** (p. 226)
48b Medulla PD− 49

49a (48b) Plant large, loosely fastened to tree bark or rock. Cylindrical isidia, granular isidia, or dactyls present. Medulla C+ red (lecanoric acid) **63. P. tinctorum** (p. 218)
49b Plant small, strongly fastened to rock. Only dactyls or coarse isidia present. Medulla C+ or C− 50

50a (49b) Medulla C+ red (lecanoric acid) . . . . **54. P. stuhlmannii** (p. 211)
50b Medulla C− (physodic acid) . . . . **64. P. tsavoensis** (p. 220)

51a (47b) Thallus yellow (usnic acid present) . . . . **69. P. xanthina** (p. 224)
51b Thallus grey (usnic acid absent) 52

52a (51b) Upper cortex with a reticulate pattern of maculae and cracks. Rhizines in part squarrose . . . . **57. P. subisidiosa** (p. 214)
52b Upper cortex without a reticulate pattern of maculae and cracks. Rhizines not squarrose 53

53a (52b) Medulla pigmented pale to bright yellow or orange 54
53b Medulla white, at most with patches of an ochraceous, K+ purple pigment near the lower cortex 55

54a (53a) Medulla pigmented bright yellow to orange throughout. Cylindrical isidia present. Coastal species . . . . **61. P. sulphurata** (p. 217)
54b Medulla pigmented pale yellow, pigment sometimes inapparent. Open dactyls present. Lower montane forest species . . . . **13. P. cryptoxantha** (p. 175)

55a (53b) Isidia flattened, dorsiventral. Gyrophoric acid present **44. P. planatilobata** (p. 203)
55b Isidia cylindrical. Chemistry various 56

56a (55b) Upper side distinctly maculate 57
56b Upper side emaculate or faintly maculate 58

57a (56a) Rhizines dimorphous. Salazinic acid and norlobaridone present. Upland species **60. P. subtinctoria** (p. 216)
57b Rhizines uniform. Stictic and norstictic acids present. Coastal species **30. P. kwalensis** (p. 191)

58a (56b) Thallus coriaceous. Isidia mainly laminal, never becoming sorediate 59
58b Thallus usually membranaceous. Isidia mainly submarginal, often becoming sorediate-granular 60

59a (58a) Medulla C+ rose, PD−, UV− (gyrophoric acid) . **47. P. pseudocrinita** (p. 205)
59b Medulla C−, PD+ orange, UV+ intensely yellow (salazinic acid, lichexanthone) **66. P. ultralucens** (p. 221)

60a (58b) Upper cortex usually continuous. Isidia rarely sorediate. Medulla PD+ orange (stictic acid) . . . . **11. P. crinita** (p. 173)
60b Upper cortex fragile and flaking. Isidia often sorediate. Medulla PD− 61

61a (60b) Medulla C+ rose, UV− (gyrophoric acid) . . . . . . **33. P. lophogena** (p. 194)
61b Medulla C−, UV+ (alectoronic acid) . . . . **36. P. mellissii** (p. 197)

Isidia absent. Soralia present

62a (46b) Marginal cilia absent 63
62b Marginal cilia present 73

63a (62a) Plant saxicolous 64
63b Plant corticolous 67

64a (63a) Medulla PD+ orange-red (protocetraric acid) . . . . . **39. P. pardii** (p. 199)
64b Medulla PD− 65

65a (64b) Medulla C− (fatty acids) . . . . . **46. P. praesorediosa** (p. 205)
65b Medulla C+ red (lecanoric acid) 66

66a (65b) Thallus small, coriaceous, strongly attached. Upper cortex emaculate, shiny **14. P. defecta** (p. 176)
66b Thallus usually large, relatively thin, loosely attached. Upper cortex faintly maculate, often matt . . . . . **7. P. austrosinensis** (p. 171)

67a (63b) Thallus yellow or yellowish grey (usnic acid present). Medulla PD+ orange-red (protocetraric acid) 68
67b Thallus pale grey (usnic acid absent). Medulla PD+ or PD− 70

68a (67a) Thallus bright yellow to yellow-green. Atranorin absent . . . **5. P. aprica** (p. 169)
68b Thallus yellowish grey. Atranorin present 69

69a (68b) Echinocarpic acid and various unknowns present . . . **15. P. dilatata** (p. 177)
69b Echinocarpic acid and unknowns absent . . . . . **49. P. rava** (p. 207)

70a (67b) Medulla C+ red (lecanoric acid) . . . . **7. P. austrosinensis** (p. 171)
70b Medulla C− 71

71a (70b) Medulla PD− (fatty acids) . . . . . **46. P. praesorediosa** (p. 205)
71b Medulla PD+ orange or red 72

72a (71b) Medulla K+ red (salazinic acid) . . . . . **12. P. cristifera** (p. 173)
72b Medulla K+ sordid brown (protocetraric acid) . . . . . **22. P. gardneri** (p. 183)

73a (62b) Upper cortex fragile and flaking. Soralia erupting in a pustular fashion or more or less mixed with isidia 74
73b Upper cortex continuous. Soralia rarely pustular, isidia absent 77

74a (73a) Medulla pigmented pale yellow. Echinocarpic acid and fatty acids present **13. P. cryptoxantha** (p. 175)
74b Medulla white. Chemistry otherwise 75

75a (74b) Medulla PD+ orange, UV− (stictic acid) . . . . . **8. P. bangii** (p. 171)
75b Medulla PD−, UV+ (alectoronic acid) 76

76a (75b) Soralia pustular, without isidia . . . . . **51. P. rimulosa** (p. 209)
76b Soralia not pustular, but here and there interspersed with isidia . **36. P. mellissii** (p. 197)

77a (73b) Medulla pigmented yellow, salmon pink, or ochraceous, pigment K− 78
77b Medulla white, at most with patches of an ochraceous, K+ purple pigment near the lower cortex 79

78a (77a) Medulla C+ red in upper parts (gyrophoric acid) . . . . **41. P. permutata** (p. 201)
78b Medulla C− (fatty acids) . . . . . **6. P. araucariarum** (p. 170)

79a (77b) Upper cortex with a reticulate pattern of maculae and cracks. Rhizines in part squarrose . . . . . **50. P. reticulata** (p. 208)
79b Upper cortex without a reticulate pattern of maculae and cracks. Rhizines not squarrose 80

80a (79b) Underside with a distinct, white marginal zone 81

80b Underside with a brown or mottled marginal zone 84

81a (80a) Lobes deeply divided, with sublinear laciniae. Medulla K+ red, PD+ orange (norstictic, galbinic, and salazinic acids). Coastal species . **38. P. parahypotropa** (p. 198)
81b Lobes more or less rounded, sublinear laciniae absent. Medulla K−, PD−. Inland species 82

82a (81b) Underside black in the centre, white peripherally. Medulla UV− (norlobaridone and/or protolichesterinic acid) . . . . **24. P. hababiana** (p. 184)
82b Underside almost entirely white. Medulla UV+ or UV− 83

83a (82b) Medulla UV+ (alectoronic acid) . . . . **34. P. louisianae** (p. 195)
83b Medulla UV− (protolichesterinic acid) . . . . **72. P. sp.B** (p. 226)

84a (80b) Rhizines dimorphous, often extending to the margins 85
84b Rhizines uniform, rarely extending to the margins 86

85a (84a) Soralia marginal. Medulla PD+ orange, KC− (salazinic acid) or PD−, KC+ red (norlobaridone) . . . . **59. P. subsumpta** (p. 215)
85b Soralia laminal. Medulla PD−, KC− (fatty acids) . . . . . . **43. P. pilosa** (p. 202)

86a (84b) Upper cortex distinctly maculate 87
86b Upper cortex emaculate or faintly maculate 88

87a (86a) Medulla UV+ (alectoronic acid, ± α-collatolic acid, ± gyrophoric acid) **32. P. lobulascens** (p. 192)
87b Medulla UV− (gyrophoric acid and/or norlobaridone, ± norstictic acid) **58. P. subschimperi** (p.214)

88a (86b) Plant saxicolous 89
88b Plant normally corticolous 91

89a (88a) Medulla UV+ (alectoronic acid) . . . . **45. P. poolii** (p. 203)
89b Medulla UV− 90

90a (89b) Medulla PD− (protolichesterinic acid) . . . . **23. P. grayana** (p. 184)
90b Medulla PD+ orange-red (fumarprotocetraric and protocetraric acids) **48. P. pseudograyana** (p. 206)

91a (88b) Medulla PD+ orange to red 92
91b Medulla PD− (but soralia may be PD+ sulphur yellow) 96

92a (91a) Protocetraric acid present 93
92b Protocetraric acid absent 95

93a (92a) Medulla C+ rose. Gyrophoric acid present . . . . . . **67. P. umbrosa** (p. 222)
93b Medulla C−. Gyrophoric acid absent 94

94a (93b) Cilia well developed. Medulla UV+ (alectoronic or α-collatolic acid) or UV− (protolichesterinic acid) . . . . **55. P. subarnoldii** (p. 212)
94b Cilia poorly developed, present only in the lobe axils. Medulla UV− (± undetermined fatty acids) . . . . **22. P. gardneri** (p. 183)

95a (92b) Stictic acid present . . . . **40. P. perlata** (p. 200)
95b Salazinic acid present . . . . **12. P. cristifera** (p. 173)

96a (91b) Soralia PD+ sulphur yellow (psoromic acid) . . . . . **16. P. direagens** (p. 178)

96b Soralia PD− or at most PD+ pale yellow (psoromic acid absent) 97

97a (96b) Medulla UV+ (alectoronic acid) . . . . **45. P. poolii** (p. 203)
97b Medulla UV− 98

98a (97b) Medulla C− (norlobaridone and/or protolichesterinic acid) **24. P. hababiana** (p. 184)
98b Medulla C+ red 99

99a (98b) Lecanoric acid present . . . . **10. P. cooperi** (p. 172)
99b Gyrophoric acid present 100

100a (99b) Soralia often ciliate, soredia granular. Fatty acids present . . **33. P. lophogena** (p. 194)
100b Soralia eciliate, soredia farinose. Fatty acids absent 101

101a (100b) Norlobaridone present . . . . **27. P. indoafra** (p. 187)
101b Norlobaridone absent . . . . **52. P. sancti-angelii** (p. 210)

Descriptions of the species

1. **Parmelia abessinica** Nyl. ex Krempelh.

Linnaea **41** : 140 (1877).—*Parmotrema abessinicum* (Nyl. ex Krempelh.) Hale, *Phytologia* **28** : 334 (1974). Type: Abessinia, leg. *Hildebrandt* (G—holotype). [TLC (Winnem 1974) : norlobaridone, loxodin, protolichesterinic acid, atranorin.]

Thallus corticolous, more or less coriaceous, adnate to loosely attached, pale grey. Lobes 0·5–1 cm broad, margins ascending, crenate, ciliate, cilia 0·5–1·5 (2) mm long. Upper side faintly to distinctly maculate, rugose and cracked with age. Medulla white. Underside rugose, sparsely rhizinate, black in the centre, with a brown, mottled, or white marginal zone. Soralia and isidia absent. Apothecia common, often crowded, stipitate, up to 1 cm in diameter, thalline margin smooth to crenulate, eciliate (or very rarely ciliate), disc perforate, spores 15–18 (20) × 8–10 μm. Conidia weakly sublageniform, 6–8 μm long.

TLC: (1) norlobaridone, ± loxodin, protolichesterinic acid, atranorin, (2) norlobaridone, ± loxodin, atranorin, (3) protolichesterinic acid, atranorin, (4) fatty acids of the reddenda type, atranorin.

Two specimens, 3K 23/124 and Nordal INB 820, from Kenya and Tanzania respectively, belong to a hitherto undescribed chemotype. They have the same general habit as *P. abessinica*, spores in the same size range, and similar conidia, and differ only in producing unnamed fatty acids of the reddenda type in the medulla. An additional specimen of this chemotype has been seen from Zaîre (LD). The same chemical properties are found in *P. mesotropa* Müll. Arg., described from Paraguay, but that species lacks cilia and has imperforate apothecia.

Parmelia glaucocarpoides Zahlbr., based on *P. glaucocarpa* Müll. Arg., non Ach., and described on material from Madagascar (G—holotype), was regarded by Hale (1965) as synonymous with *P. abessinica*. Its morphology is similar, it has sublageniform conidia 5–6 μm long, and contains protolichesterinic acid, but the spores are 25–27 (30) × 12–15 μm and fairly thick-walled, showing that *P. glaucocarpoides* should be regarded as a species distinct from *P. abessinica*.

Parmelia abessinica is a common and widespread species of dry, well lit sites at intermediate altitudes, such as bushed grassland, artificial habitats, open hillsides, and the edge of forests. It has been collected between 900 and 2600 m, but is most common below 2000 m. Outside our area it is known from South and West Africa and Mexico (Hale, 1965).

Selected East African records

Ethiopia. Sidamo Province, Yirga Alem, *Winnem* 477/1 (O). **Kenya.** Eastern Province, Marsabit District, Mt Marsabit, vicinity of Lake Paradise, 4K 6/124: Kitui District, Mutomo, 50 km NE of Kibwezi, K 21/2; Machakos District, Ol Doinyo Sapuk, 20 km SE of Thika, 2K 1/101, lava flow 5 km

NW of Kibwezi, 2K 22/101, 5K 2/31; Embu District, Izaak Walton Inn, K 53/8; Meru District, between Chogoria and South Mara River, 3K 11/104. Rift Valley Province, Kajiado District, Chyulu Hills, K 39/13; Samburu District, WSW slope of Warges, 4K 3/101; Laikipia District, Burguret, 4K 25/108; Nakuru District, Eastern Mau Forest 8 km ENE of Mau Narok, 4K 32/109, Lake Naivasha Hotel, on east shore of lake, 3K 21/14. Coast Province, Taita District, near school W of Wundanyi, 2K 27/101. Western Province, Kakamega District, Kakamega Forest by River Ikuyawa, 4K 10/101. **Tanzania.** Lake Province, Mosuma District, near Fort Ikomo Lodge, *Sipman* 6357 (herb. Sipman). Northern Province, Arusha District, Arusha National Park, Juniper Hill, T 3/114, Mt Meru Crater, T 5/162; Mbulu District, Babati, *Sitari* 541 (TUR). Southern Highlands Province, Njombe District, 12 km SE of Njombe, *Nordal* INB 820 (O). **Uganda.** Kigezi District, Bufumbira County, Kisoro, Travellers' Rest Hotel, U 19/3, 3U 59/10; Ruzhumbura County, W edge of Maramagambo Forest, 2U 11/6. Karamoja District, Matheniko County, near Sogolomon on Mt Moroto, 2U 36/53, NW of Mt Moroto, 4 km SW of Nakiloro, 2U 38/6.

2. Parmelia aldabrensis Dodge. **Fig. 2**

Ann. Mo. bot. Gdn **46** : 160 (1959).—*Parmotrema aldabrense* (Dodge) Hale, *Phytologia* **28** : 334 (1974). Type: Aldabra Group, coll. *Walter Fox* 220 (BM—holotype). [TLC (Winnem 1974): norstictic acid.]

Thallus corticolous, adnate, pale grey to grey-green. Lobes 0·5–0·8 cm broad, deeply divided, margins ascending, crenate, ciliate, cilia up to 2·5 mm long. Upper side distinctly maculate. Medulla white. Underside smooth or somewhat rugose, medium to dark brown, rarely with a white mottled marginal zone, rhizines slender, scattered almost to the margins. Soralia and isidia absent. Apothecia numerous, marginal and submarginal, often eccentrically orientated on semitubular stipes, disc 0·5–1 (1·5) cm in diameter, with a small perforation, thalline margin smooth or weakly crenate, occasionally ciliate, spores 13–17 × 5–8 μm. Conidia filiform, 12–15 μm long.

TLC: norstictic acid, stictic acid.

All East African specimens contained stictic and norstictic acids, but the type specimen, as well as two other specimens from the Aldabra Islands, *Stoddart* 992 (BM) and *Fosberg* 49319 (S), had only norstictic acid. Morphologically the two populations are the same. No apothecia or conidia were found in the holotype, but the collection *Stoddart* 992 had spores

Fig. 2 *Parmelia aldabrensis* Dodge, 3K 30/110 (O). Rule = 1 cm.

12–16 × 6–7 μm and filiform conidia 10–12 μm, which agrees well with the East African material.

Parmelia preperforata W. Culb., described from Texas (US—holotype), is chemically concordant with the East African specimens of *P. aldabrensis*, has a maculate upper cortex, marginal to submarginal apothecia, and similar spores and conidia. It differs in having broadly rounded lobes which are not particularly deeply divided, and an underside which is black in the centre with a wide, pale ivory marginal zone.

Parmelia aldabrensis is locally abundant in mangroves by the Indian Ocean, where it often grows convoluted around thinner branches. It has also been collected in the lowlands of Tanzania up to 1000 m. Outside our area it is known from the Aldabra Islands and Madagascar (Hale, 1965).

East African records

Kenya. Coast Province, Kwale District, 2 km N of Gazi, K 44/2, 111, 3K 30/45, 110; Kilifi District, Mida Creek, 3K 27/104, 3K 29/106, Gedi ruins, 3K 25/104. **Tanzania.** [? Tanga Province] Masaihochland, Wadiboma, *Fischer* 703 (G, type of *P. hildebrandtii* var. *ciliata* Müll. Arg.). Eastern Province, Mzizima [Uzaramo] District, Kunduchi, *Bjørnstad* AB 1942 (O); Morogoro District, Mindu Forest Reserve, 4 May 1978, *Dahl* (O).

3. Parmelia amaniensis Steiner & Zahlbr. **Fig. 3**

Bot. Jb. **60** : 526 (1926). [Tanzania] Im Regenwald bei Amani, Ost-Usambara, 800 m, July 1909, leg. *Brunnthaler* (W—holotype). [TLC: alectoronic acid, protocetraric acid, atranorin.]

Parmelia pachyspora Hale, *Contr. U.S. natn. Herb.* **36** (5) : 299 (1965).—*Parmotrema pachysporum* (Hale) Hale, *Phytologia* **28** : 338 (1974). Type: Angola, Huila, 10 km N of Sá de Bandeira, 3 February 1960, leg. *G. Degelius* (herb. Degelius—holotype). [TLC: α-collatolic acid, alectoronic acid (+), protocetraric acid, atranorin.]

Thallus corticolous, membranaceous to more or less coriaceous, loosely attached, pale grey. Lobes 0·5–1·5 cm broad, crenate, ciliate, cilia 3–5 (7) mm long. Upper side emaculate.

Fig. 3 *Parmelia amaniensis* Steiner & Zahlbr., *Ryvarden* 11632 (O). Rule = 1 cm.

Medulla white. Underside black, with a narrow brown or rarely white mottled marginal zone, rhizines sparse. Soralia and isidia absent. Apothecia up to 1·7 cm in diameter, submarginal on swollen stipes which become somewhat constricted with age, or marginal and eccentrically situated on semitubular, convoluted lobes, thaline margin normally lobulate-dentate and ciliate, disc imperforate, spores thick-walled, 25–40 × 15–18 μm. Conidia weakly sublageniform, 5–8 μm long.

TLC: (1) alectoronic acid, protocetraric acid, atranorin, (2) α-collatolic acid, ± alectoronic acid (trace), protocetraric acid, atranorin, (3) ± protolichesterinic acid, protocetraric acid, atranorin.

Overlooking the presence of protocetraric acid, Hale (1965) reduced *P. amaniensis* to synonymy with *P. subrugata* Krempelh., a South American species with alectoronic and α-collatolic acids. In the same work he described the new species *P. pachyspora,* with protocetraric acid as its diagnostic medullary substance. Later, under the description of the new species *P. paradoxa* (Hale, 1973), he noted that *P. pachyspora* was now known to contain alectoronic acid in addition to protocetraric acid. When subjecting the type specimens to TLC we found that *P. amaniensis* contained alectoronic acid and *P. pachyspora* mainly α-collatolic acid in addition to protocetraric acid. Since anatomy, morphology, and ecological requirements are the same for the two species, we here reduce *P. pachyspora* to synonymy with *P. amaniensis.* We also include in the species some specimens which produced protocetraric acid ± protolichesterinic acid in the medulla (Table 12).

In our area the typical strain has been collected in Tanzania, the *pachyspora* strain in Uganda, and strain (3) in both countries.

Parmelia amaniensis has been found in the lower montane forests between 800 and 1150 m altitude, with the exception of one collection from 2000 m. In East Africa we have seen specimens from Tanzania and Uganda. Outside our area the species occurs in Angola, Malawi, Moçambique, Sierra Leone, Zambia and Zimbabwe. It seems to be restricted to Africa.

East African records

Tanzania. Eastern Province, Morogoro District, Nguru Mountains, E slope above Kwamanga village near Mhonda Mission, *Pócs & Mabberley* 6397/H (herb. Pócs), Uluguru Mountains, N slope of Bondwa above Morogoro, *Pócs* 6732 (herb. Pócs). Tanga Province, Tanga District, East Usambara Mountains, Amani Forest Reserve, *T. & S. Pócs* 6100/AD–B (herb. Pócs); Lushoto District, in rain forest by Amani, East Usambara, *Brunnthaler* 7/1909 (W—holotype of *P. amaniensis*), Usambara Mts, Amani, Karimi Estate (road towards Monga), *Moberg* 1485b (UPS). **Uganda.** Masaka District, Bukoto County, Jubiya Forest, 3U 28/18, 3U 32/3, *Lye* L 604A (herb. Lye), N edge of Malabigambo Forest, 3U 25/4.

4. **Parmelia andina** Müll. Arg.

Revue mycol. **1** : 169 (1879).—*Parmotrema andinum* (Müll. Arg.) Hale, *Phytologia* **28** : 334 (1974). Type: prope Cisne, Ecuador, 2800 m, leg. *Ed. André* 4324 bis (G—holotype, BM—isotype). [TLC (Winnem 1975): lecanoric acid, atranorin.]

Parmelia modesta Hue, *Bull. Soc. Bot. France 63, Mém.* **6** (28) : 6 (1916). Type: Afrique equatoriale anglaise, 1912, leg. *Vte de Poncins,* (PC—holotype). [TLC: lecanoric acid, atranorin.]

Thallus corticolous or rarely saxicolous, coriaceous, loosely attached, pale grey, medium grey, or grey-green. Lobes up to 2 cm broad, rounded, entire or crenate, eciliate. Upper side usually matt, faintly to distinctly maculate (especially in the vicinity of the apothecia), pitted, folded, or rugose towards the centre. Medulla white. Underside black, matt and rugose, with a white, brown, or mottled marginal zone, rhizines short, black in central parts, pale brown or white peripherally, unevenly distributed. Soralia and isidia absent. Apothecia submarginal to laminal, often numerous, sometimes crowded and obscuring the thallus, 1–3 (4) cm in diameter, thalline exciple rugose, strongly maculate, disc widely perforate, spores 13–18 × 8–10 μm. Conidia filiform, 10–16 (20) μm long.

TLC: lecanoric acid, atranorin.

Parmelia andina differs from *P. hololoba* mainly in the absence of cilia. When *P. hololoba* extends inland and occurs in the same habitats as *P. andina*, its cilia sometimes become sparse, short, and stunted, so that the two species are almost indistinguishable.

Parmelia andina is common and widespread in dry, well lit sites, such as savannas, open hillsides, and artificial habitats. It has been collected between 900 and 2400 m altitude in all four countries of our studies. Outside our area it is known from numerous localities in continental Africa as well as from Madagascar, India, Thailand, Tahiti, and South America (Hale, 1965).

Selected East African records
Ethiopia. See Winnem (1975). **Kenya.** Eastern Province, Isiolo District, 8 km S of Isiolo, 4K 28/101; Machakos District, Kilima Kiu, 5K 3/2; Embu District, Embu, Izaak Walton Inn, K 53/109; Meru District, vicinity of Chogoria, 3K 9/104; Marsabit District, *c.* 1 km N of the mountain Ajaumarka, *Moberg* 3864 (UPS). Rift Valley Province, Elgeyo Marakwet District, 8 km NE of Kapcherop, 2K 15/114; Nakuru District, E of road by Lake Elmenteita, 2K 20/101; Samburu District, WSW slope of Warges, 4K 3/106. Western Province, Kakamega District, Kakamega Forest by River Ikuyawa, 4K 10/105. Nyanza Province, Kisii District, 1 km SE of Kisii, 4K 12/114. Central Province, Nyeri District, Mt Kenya Safari Club, 4K 19/112. **Tanzania.** Northern Province, Arusha District, Arusha National Park, Kusare Forest, T 2/120. Eastern Province, Morogoro District, above Morningside in the Uluguru Mts, 6 May 1978, *Dahl* (O). Southern Highlands Province, Iringa District, Ruaha National Park, summit of Magangwe Hill. *Bjørnstad* 1780–a (O). Southern Province, Songea District, Gumbiro, *Nordal* INB 849 (O). **Uganda.** W. Mengo District, Kyadondo County, Makerere University Campus, U 1/7b, *Manum* 1/1968 (O); Busiro County, Entebbe Botanical Garden, U 9/56b. Toro District, Burahya County, Fort Portal, *Dale* 144 (BM—type of *P. dalei* Dodge); Busongora County, 10 km NW of Kilembe, 2U 12/22. Karamoja District, Matheniko County, south side of Mt Moroto, 2U 35/4. West Nile District, Mt Otse, 1962, *Thomas* (BM—type of *P. thomasii* Dodge).

5. Parmelia aprica Krog & Swinscow sp. nov. **Fig. 4**

Thallus corticola, coriaceus, adnatus, flavus ad flavo-viridis. Lobi 0·5–1 cm lati, eciliati, marginibus

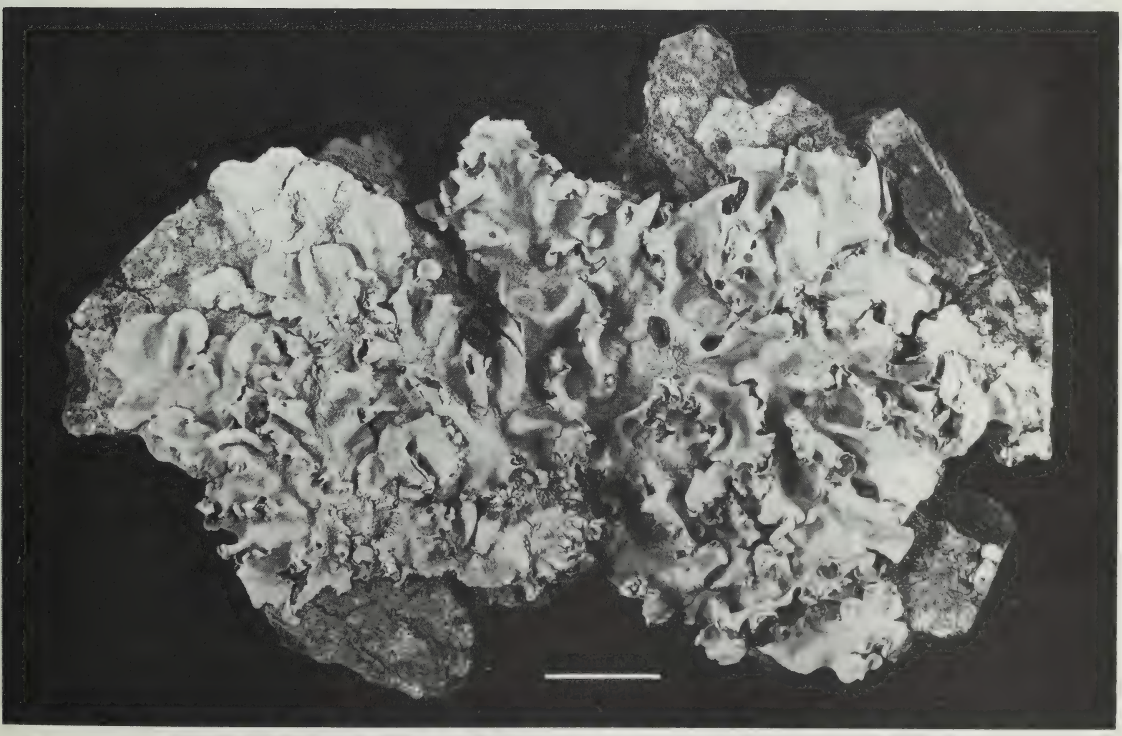

Fig. 4 *Parmelia aprica* Krog & Swinscow, holotype (O). Rule = 1 cm.

integris vel leniter crenatis, superne emaculati, rugescentes, rimosi, Soralia marginalia, ad lobos peripherales linearia, ad lobos ascendentes laterales subcapitata, aliquando ad laminam extensa. Apothecia et pycnidia ignota. Acidum protocetraricum et acidum usnicum continens.

Thallus corticolous, coriaceous, adnate, bright yellow to yellow-green. Lobes 0·5–1 cm broad, eciliate, with entire or weakly crenate margins. Upper side emaculate, becoming rugose, irregularly cracked and sometimes lobulate towards the centre. Medulla white. Underside black in the centre, with a broad, brown, shiny marginal zone, rhizines sparsely developed. Soralia marginal, linear on peripheral lobes and subcapitate on ascending lateral lobes, sometimes spreading diffusely on to the lamina. Soredia granular, pale green to yellowish. Apothecia and pycnidia unknown.

TLC: protocetraric acid, ± traces of fatty acids, usnic acid.

Type: Kenya. Eastern Province, Machakos District, lava flow 5 km NW of Kibwezi, 2° 35′ S, 37° 51′ E, 1000 m altitude, on shrubs, January 1972, coll. *H. Krog & T. D. V. Swinscow* no. K 20/103 (O—holotype; BM, UPS—isotypes).

Parmelia aprica differs from both *P. rava* and *P. dilatata* in its bright yellow colour, yellow-green soredia, and the absence of atranorin in the cortex; it differs from *P. dilatata* also in the absence of echinocarpic acid and associated substances.

Parmelia vivida, newly described in this work, appears to be the corresponding primary species. It has spores 20–22 × 8–10 μm and sublageniform conidia 6–7 μm long.

Parmelia aprica is known only from the type locality, where it grew on shrubs in a rather dry site exposed to high light intensity. Further collection numbers are 2K 22/105 and 3K 23/1, 129.

6. Parmelia araucariarum Zahlbr.

Denkschr. Akad. Wiss., Wien, math.-nat. Kl. **83** : 179 (1909).—*Parmotrema araucariarum* (Zahlbr.) Hale, *Phytologia* **28** : 334 (1974). Type: Brasilia. Prov. Sao Paulo. Prope S. Amaro in circuitu urbis S. Paulo, 800 m, May 1901, leg. *V. Schiffner* (W—holotype, O—isotype). [TLC: pigment, fatty acids in the reddenda complex, atranorin.]

Thallus corticolous, membranaceous, loosely attached, green-grey. Lobes 0·5–1·5 cm broad, ciliate, cilia 1–2 (3) mm long. Upper side emaculate, more or less irregularly cracked in older parts. Medulla distinctly pigmented salmon pink, yellow, or ochraceous, pigment K—. Underside black, with a brown, naked marginal zone, rhizines sparse. Soralia marginal, linear. Mature apothecia not seen, but the holotype specimen has one immature, imperforate apothecium with a sorediate thalline margin. Conidia sublageniform, 6–8 μm long.

TLC: pigment, ± protolichesterinic acid, atranorin.

Parmelia araucariarum was described as an eciliate species by both Zahlbruckner (1909) and Hale (1965). Later, Hale (1974*a*) noted that cilia might be very sparsely developed. In fact, short cilia are present in an isotype in O, and the holotype, on close examination, also possesses one or two elusive cilia. The East African specimens are distinctly ciliate with most cilia less than 2 mm but occasionally reaching 3 mm in length. The species should be regarded as normally ciliate, and does probably not represent the sorediate counterpart of *P. myelochroa* Hale as suggested by Hale (1965).

The type specimens contain different fatty acids from those of the East African specimens. We regard this as a minor chemical variation of no taxonomic consequence.

Parmelia araucariarum is rare in East Africa. We have collected it twice in Kenya where it was growing in the lower montane forest on the south and east slopes of Mt Kenya at 2000–2100 m. The species was previously known only from the type locality in Brazil.

East African records

Kenya. Central Province, Kirinyaga District, Mt Kenya, 2 km NW of Irangi Forest Station, moist deciduous forest near River Ena, K 48/111. Eastern Province, Meru District, Mt Kenya, open forest on east side, at Themwe, 3K 16/104, 108.

7. Parmelia austrosinensis Zahlbr.

Symb. sin **3** : 192 (1930).—*Parmotrema austrosinense* (Zahlbr.) Hale, *Phytologia* **28** : 335 (1974). Type: China, Kveitschou, Gwanyinschan, near Kweiyang, leg. *Handel-Mazetti* 10580 (WU—not seen).

Thallus corticolous or more rarely saxicolous, usually somewhat coriaceous, loosely attached, pale grey, ash grey, or grey-green. Lobes 1–3 cm broad, rounded, entire or crenate, eciliate, margins often ascending. Upper cortex weakly maculate, sometimes distinctly maculate, especially in central parts, more or less rugose and reticulately cracked. Medulla white. Underside black, with a white, brown, or mottled marginal zone, rhizines short, unevenly distributed. Soralia marginal and submarginal, soredia granular. Apothecia substipitate, thalline exciple sorediate, disc perforate or imperforate, spores 12–17 (20) × 7–10 μm. Conidia filiform, 10–14 μm.

TLC: lecanoric acid, atranorin.

For differences from *P. defecta,* see under that species. From *P. cooperi* it differs mainly in the absence of marginal cilia.

Parmelia austrosinensis is one of the commonest Amphigymnias in dry, well lit sites in all four countries of our study. It has been collected between 1000 and 3000 m altitude, but is most common below 2500 m. Outside our area it is a common and widespread species in tropical amd temperate regions.

Selected East African records
Ethiopia. See Winnem (1975). **Kenya.** Central Province, Kiambu District, escarpment E of Rift Valley, 35 km NW of Nairobi, K 15/121; Nyeri District, Mt Kenya, W side, Naro Moru track, K 32/120; Kirinyaga District, Mt Kenya, S side, by Thiba Fish Camp, K 52/113. Rift Valley Province, Kajiado District, Chyulu Hills, K 39/104; Elgeyo Marakwet District, 7 km N of Chebiemit, 2K 6/127; Uasin Gishu District, near Sergoi, 2K 9/112; Trans Nzoia District, by road E of Moiben, near Hoey's Bridge, 2K 12/116; Nakuru District, E of road by Lake Elmenteita, 2K 20/119; Samburu District, WSW slope of Warges, 4K 3/107; Kericho District, Cheboswa ENE of Kericho, 4K 17/113; Laikipia District, Burguret, 4K 25/113; Narok District, Enabilibil, 22 km S of Siape Bridge, 4K 31/105. Eastern Province, Embu District, 10 km N of Embu, by River Rubingazi, K 46/106; Machakos District, Ol Doinyo Sapuk, 20 km SE of Thika, 2K 1/115; Meru District, S side of Chogoria, 3K 9/106. Coast Province, Taita District, above Wundanyi, 2K 25/133. Western Province, Kakamega District, Kakamega Forest by River Ikuyawa, 4K 10/103. Nyanza Province, Kisii District, 6 km E of Keroka, 4K 11/109; Homa Bay District, 7 km WSW of Ringa, 4K 14/102. **Tanzania.** Northern Province, Arusha District, Arusha National Park, Kusare Forest, T 2/116. Eastern Province, Morogoro District, above Morningside in the Uluguru Mts, 6 May 1978, *Dahl* (O). Southern Highlands Province, Njombe District, between Kitulo and Matamba, 9 May 1978, *Dahl* (O). **Uganda.** Karamoja District, Matheniko County, southern slopes of Mt Moroto, 2U 35/9; Dodoth County, Kidepo Valley National Park, 3U 15/112. W. Mengo District, Busiro County, Entebbe Botanical Garden, 3U 5/20. Kigezi District, Bufumbira County, 2 km W of Kanaba Gap, 3U 58/7.

8. Parmelia bangii Vainio

in Schmidt, *Bot. Tidsskr.* **29** : 104 (1909).—*Parmotrema bangii* (Vainio) Hale, *Phytologia* **28** : 335 (1974). Type: Lichens of South America No. 13, Bolivia, La Paz, 1891, *M. Bang* (H-NYL 35500—holotype). [TLC: stictic acid, constictic acid, atranorin.]

Thallus corticolous, membranaceous, loosely attached, pale green-grey. Lobes 0·5–1 cm broad, crenate, sparingly ciliate, cilia 0·5–1 (2) mm long. Upper cortex emaculate, fragile, cracking and flaking, folded and rugose towards the centre. Medulla white. Underside smooth, shiny, black, with a pale brown marginal zone, rhizines mostly dense, in some places reaching almost to the margins. Soralia developing as pustules in a broad submarginal zone, soredia granular. Apothecia not seen in East African material. (In the holotype apothecia are subsessile, thalline exciple sorediate, disc imperforate, spores 30–40 × 15–20 μm, thick-walled.) Conidia rod-shaped to shortly filiform, 8–10 μm long.

TLC: stictic acid, constictic acid, atranorin.

Parmelia bangii has been collected in inselbergs and montane forests in Kenya between 1500 and 3200 m altitude. It was previously known from two localities in Bolivia and Colombia respectively (Hale, 1965) and from Tenerife, the Canary Islands (Østhagen & Krog, 1976).

East African records

Kenya. Eastern Province, Fort Hall District, Aberdare Mountains, Kimakia Forest Station, *Ryvarden* 9028 c (O); Machakos District, Ol Doinyo Sapuk, 20 km SE of Thika, 2K 4/101; Marsabit District, Mt Marsabit, W side of Sokorte Dika 'swamp-lake', *Lye* L 661 (herb. Lye); Meru District, Mt Kenya, N slope, Sirimon track, 4K 20/127. Central Province, Embu District, Embu, by Izaak Walton Inn, 3K 6/130. Rift Valley Province, Kajiado District, Ngong Hills, K 45/118. Coast Province, Taita District, near school W of Wundanyi, 2K 26/101, 2K 27/102; Taita District, Taita Hills, Mt Iyale, *Nordal* INB 725 (O).

9. Parmelia cetrata Ach.

Syn. Lich.: 198 (1814).—*Parmotrema cetratum* (Ach.) Hale, *Phytologia* **28** : 335 (1974). Type: Ad corticem arborum in America septentr. (not seen).

Thallus corticolous, membranaceous to somewhat coriaceous, medium grey to green-grey. Lobes up to 1·5 cm broad, rounded, crenate or deeply incised, the laciniae 1–3 mm broad, with truncate apices, ciliate, cilia 1–2 mm long. Upper cortex reticulately maculate and cracked. Medulla white. Underside smooth, black, with a dark brown marginal zone, densely rhizinate, often with rhizines and papillae to the margins, rhizines mainly simple, but occasionally squarrose. Soralia and isidia absent. Apothecia stipitate, thalline exciple entire, disc perforate, spores 11–13 × 8–10 μm. Conidia filiform, 10–14 μm long.

TLC: salazinic acid, atranorin (+).

Parmelia cetrata, a widespread temperate species, is rather rare in East Africa. It has been collected in inselbergs and upland habitats which are generally well lit but periodically influenced by mist. We have found it in Kenya and Tanzania between 1400 and 2000 m altitude, with the exception of one collection from 2600 m.

East African records

Kenya. Eastern Province, Marsabit District, Mt Marsabit, vicinity of Lake Paradise, 4K 6/131; Machakos District, Ol Doinyo Sapuk, 20 km SE of Thika, 2K 1/104, 2K 2/125, Mua Hills, 3K 2/120. Coast Province, Taita District, near school W of Wundanyi, 2K 26/102, 2K 27/105. **Tanzania.** Northern Province, Arusha District, Arusha National Park, Juniper Hill, T 3/113, Mt Meru Crater, T 5/117.

10. Parmelia cooperi Steiner & Zahlbr.

in Zahlbruckner, *Bot. Jb.* **60** : 528 (1926). Type: South Africa, Kapland, Kapprana, *Cooper* 1813 (W—holotype, not seen).

Thallus corticolous or rarely saxicolous, membranaceous to coriaceous, loosely attached, pale grey to grey-green. Lobes more or less revolute, 0·8–2 cm broad, rounded, entire or crenate, ciliate, cilia coarse or slender, (0·3) 2–5 mm long. Upper side emaculate or faintly maculate, more rarely distinctly maculate, reticulately cracked towards the centre. Medulla white. Underside black to the margins or with a brown or mottled marginal zone, rhizines short, sparse, unevenly distributed. Soralia marginal and submarginal, soredia granular. Only immature apothecia seen in the East African material. (According to the protologue the spores are 15–19 × 7–9 (10) μm.) Conidia shortly filiform, 10–12 (14) μm long.

TLC: lecanoric acid, atranorin.

Parmelia cooperi is believed to be the sorediate counterpart of *P. hololoba.* They seem to have about the same ecological requirements, preferring dry, well lit sites at low and intermediate altitudes. However, *P. cooperi* has not been found on the coast, while it extends to higher elevations than *P. hololoba.* It has been collected between 1500 and 3000 m, but is most common below 2400 m. The species is known from continental Africa south of Sahara, Madagascar, and India.

Selected East African records
Ethiopia. See Winnem (1975). **Kenya.** Central Province, Kiambu District, escarpment E of Rift Valley, 35 km NW of Nairobi, K 15/3, 103; Nyeri District, Mt Kenya Safari Club, 4K 19/114; Kirinyaga District, Irangi Forest Station, 5K 4/9a. Eastern Province, Machakos District, Mua Hills, 3K 2/110; Meru District, Mt Kenya, E side, at Themwe, 3K 16/191; Marsabit District, Mt Marsabit, NW side of Lake Paradise, *Lye* L 657A (herb. Lye). Rift Valley Province, Nakuru District, Londiani Forest SE of Mau Summit, 2K 5/103; Elgeyo Marakwet District, 7 km N of Chebiemit, 2K 6/105; Uasin Gishu District, 5 km NW of Timboroa Summit, 2K 19/129; Laikipia District, Naro Moru River Lodge, 2K 34/101. Coast Province, Taita District, above Wundanyi, 2K 25/111. **Tanzania.** Northern Province, Arusha District, Mt Meru Crater, T 5/155. Tanga Province, Lushoto District, Usambara Mts, Magamba *c.* 4 km N of Lushoto, *Ryvarden* 10911 (O). Eastern Province, Morogoro District, Uluguru Mts, Morningside Research Station, *Ryvarden* 11580 (O). Southern Highlands Province, Mbeya District, between Kimondo and Kikondo, 9 May 1978, *Dahl* (O). **Uganda.** Toro District, Busongora County, 10 km NW of Kilemba, slopes of Ruwenzori, 2U 12/45; Burahya County, 1 km N of Fort Portal, *Pentecost* RE 21 (BM). Kigezi District, Kinkizi County, Mafuga Forest, 3U 39/4.

11. Parmelia crinita Ach.

Syn. Lich.: 196 (1814).—*Parmotrema crinitum* (Ach.) Choicy, *Bull. mens. Soc. linn. Lyon* **21** : 175 (1952). Type: North America, *Muhlenberg* (H—holotype). [TLC: not tested.]

Thallus corticolous, more rarely terricolous or saxicolous, membranaceous, loosely attached, pale grey, ash grey, or grey-green. Lobes 0·5–1·5 (2) cm broad, crenate or irregularly incised, ciliate, cilia 0·5–2 (3) mm long. Upper side emaculate, smooth to faintly ridged or pitted, cortex fragile. Medulla white. Underside black, shiny, with a narrow, brown, naked marginal zone, rhizines abundant, sometimes extending to the margins. Isidia sparse to numerous, laminal and marginal, usually cylindrical, short, and slender but sometimes forming coarse, coralloid outgrowths, commonly ciliate, occasionally dissolving into soredia. Apothecia rare, submarginally situated on constricted stipes, thalline exciple rugose, isidiate, disc imperforate, spores 25–35 × 12–18 μm, thick-walled. Pycnidia not seen.

TLC: stictic acid, constictic acid, atranorin.

The vegetative propagules of *P. crinita* show a greater variation in the tropics than they do in the temperate region, to a certain extent recalling those of *P. lophogena* and *P. mellissii. Parmelia bangii,* another stictic acid producing species with large spores, is obviously very closely related to *P. crinita* as here delimited, but it is much smaller and more narrow-lobed and has submarginal, sorediate pustules which do not produce laminal cilia or intergrade with sorediate isidia.

Parmelia crinita is one of the commoner species of inselbergs, montane forests and the ericaceous zone. We have collected it between 1400 and 3400 m altitude, but most frequently between 2000 and 3000 m. It is a common and widespread species of humid habitats in temperate and tropical regions.

Selected East African records
Ethiopia. See Winnem (1975). **Kenya.** Central Province, Nyeri District, Mt Kenya, W side, Naro Moru track, several localities, Aberdare Mts, several localities. Rift Valley Province, Kajiado District, Ngong Hills, K 45/105, 518; Elgeyo Marakwet District, Chebiemit Forest 1 km W of Cheptongei, 2K 11/105; Uasin Gishu District, 5 km NW of Timboroa Summit, 2K 19/101. Eastern Province, Machakos District, Mua Hills, 3K 2/128; Meru District, Mt Kenya, E side, at Themwe, 3K 16/196, Mt Kenya, N side, Sirimon Track, 4K 20/122; Marsabit District, Mt Marsabit, vicinity of Lake Paradise, 4K 6/132. **Tanzania.** Northern Province, Arusha District, Mt Meru, several localities. Eastern Province, Morogoro District, Kitulangala Forest Reserve, 6 May 1978, *Dahl* (O). **Uganda.** Kigezi District, Rubanda County, near Rwaburimbe, U 11/2; Bufumbira County, 2 km W of Kanaba Gap, 3U 58/2b.

12. Parmelia cristifera Taylor **Fig. 5**

J. Bot., Lond. **6** : 165 (1847).—*Parmotrema cristiferum* (Taylor) Hale, *Phytologia* **28** : 335 (1974). Type: Calcutta, *Wallich* (FH—TAYL—lectotype, BM—isolectotypes). [TLC: salazinic acid, atranorin.]

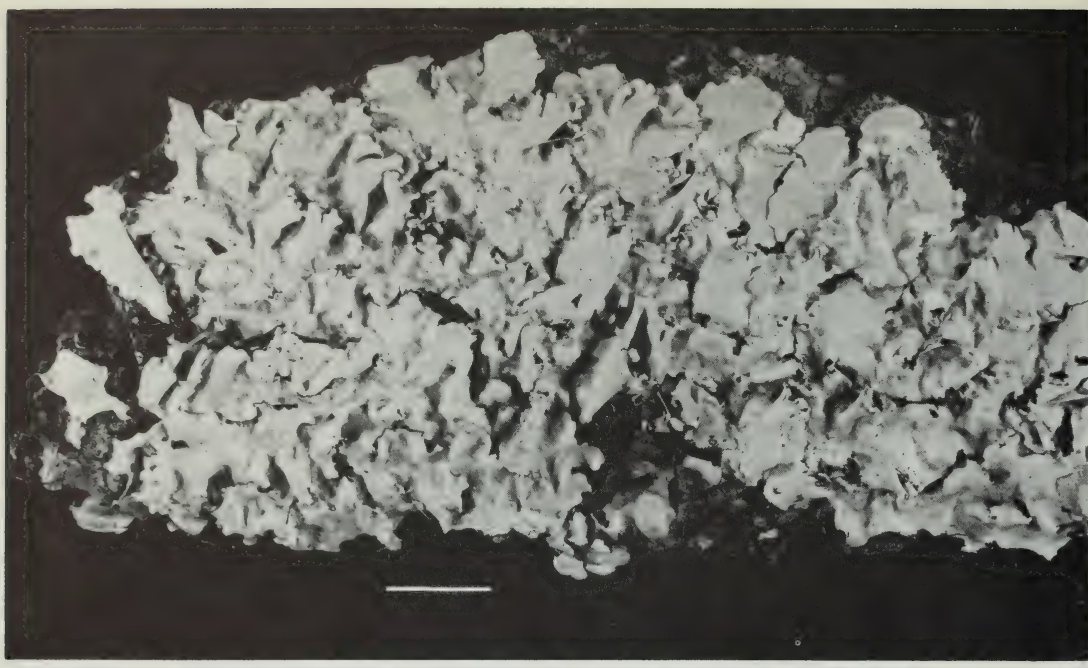

Fig. 5 *Parmelia cristifera* Taylor, K 41/107 (O). Rule = 1 cm.

Thallus corticolous, adnate to loosely attached, pale grey. Lobes 0·5–1 cm broad, rounded, entire or weakly crenate, main lobes eciliate, lateral lobes and lobe axils sparingly ciliate, cilia 0·5–1·5 mm long, or cilia absent. Upper cortex even, emaculate. Medulla white. Underside smooth, shiny, black, with a brown marginal zone, rhizines short, coarse, sparse. Soralia mainly marginal on lateral lobes, sorediate lobes more or less ascending. Apothecia not found in East African material. (An isotype in BM has small, laminal apothecia with spores 25–30 × 13–15 μm).

TLC: salazinic acid, atranorin.

In the protologue for *P. cristifera,* Taylor (1847) cited specimens from Mauritius (*Wright*), Brazil (*Gardner*), and Demerara (*Parker*), as well as from Calcutta (*Wallich*). We have not seen the Wright collection, but a specimen from Mauritius (without collector but annotated 'type material'), in the BM, clearly corresponds to the lectotype. That is also the case with another specimen from Mauritius, namely the holotype of *P. sieberi* Dodge (FH). The Gardner syntype, from Brazil, is the holotype of *P. gardneri*, while the Parker syntype, from Guyana (FH), contains fatty acids and represents *P. praesorediosa*.

The lectotype and two isolectotypes (BM) of *P. cristifera* show a species up to 30 cm in diameter, with peripheral lobes up to 3 cm broad, and with lateral, marginal, linear soralia more or less radiating towards the centre. Short, sparse marginal cilia are present in one of the isotypes. The East African specimens were on the whole much smaller and they were all sparsely ciliate.

Parmelia stuppea Taylor is another sorediate, ciliate species with salazinic acid; it has been reported from, for example, Natal and Zimbabwe (Hale, 1965). Our specimen 4K 6/133, from Mt Marsabit, may come close to that species. It had rod-shaped to shortly filiform conidia, 8–10 μm long, while those seen in North American material were rod-shaped and 5–8 μm long. However, the soralia of our specimen had a tendency to spread submarginally, while those of *P. stuppea* usually are strictly marginal.

Parmelia hildebrandtii Krempelh., an eciliate species, was placed in synonymy with *P. cristifera* by Hale (1965), but according to the protologue it has small, subglobose spores 11–15 × 11–12 μm. If the spore data are correct, the species must be considered to be distinct

from *P. cristifera*, and should perhaps be compared with *P. stuppea* (spores 12–17 × 6–9 μm), since the presence or absence of cilia seems to be a variable character in this group.

The determination of the East African specimens must be regarded as tentative until fruiting material becomes available. However, on the basis of ecological traits we doubt that the specimens from the coast represent *P. stuppea*, a largely temperate species.

The East African specimens cannot be distinguished from *P. gardneri* without a chemical test. However, in addition to the chemical difference, *P. gardneri* differs from both *P. cristifera* and *P. stuppea* in spore size.

Most of the specimens we have assigned to *P. cristifera* have been collected at about 300 m altitude in Kenya, where they grew on trees in the low coastal hills off the Indian Ocean, but we include records up to 1450 m. The species is common and widespread in the tropics and subtropics, but with relatively few records from Africa (Hale, 1965).

East African records

Kenya. Coast Province, Kwale District, Shimba Hills, 25 km SW of Mombasa, Kivumoni Forest, K 41/102, 107, Pengo Hill, *Santesson* 20914 (UPS), Kwale, Forestry Station, *Santesson* 20802a pro parte (UPS). Eastern Province, Marsabit District, Mt Marsabit, vicinity of Lake Paradise, 4K 6/133. **Tanzania.** Northern Province, Moshi District, Marangu, near Kibo Hotel, *Burnet* 123 (BM). **Uganda.** Masaka District, Bukoto County, near Kasaka in Jubiya Forest, *Lye* L605A (herb. Lye).

13. **Parmelia cryptoxantha** des Abb. **Fig. 6**

Mém. Inst. scient. Madagascar B, **10** : 115 (1961).—*Parmotrema cryptoxanthum* (des Abb.) Hale, *Phytologia* **28** : 335 (1974). Type: Madagascar. Forêt d'Ambohitanteli (30 km NE d'Ankazobe), 1600 m, *des Abbayes* (REN—lectotype, not seen).

Thallus corticolous, membranaceous, loosely attached, pale green-grey, lobe margins sometimes tinged with brown. Lobes 0·8–1·2 cm broad, rounded, entire or crenate, ciliate, cilia

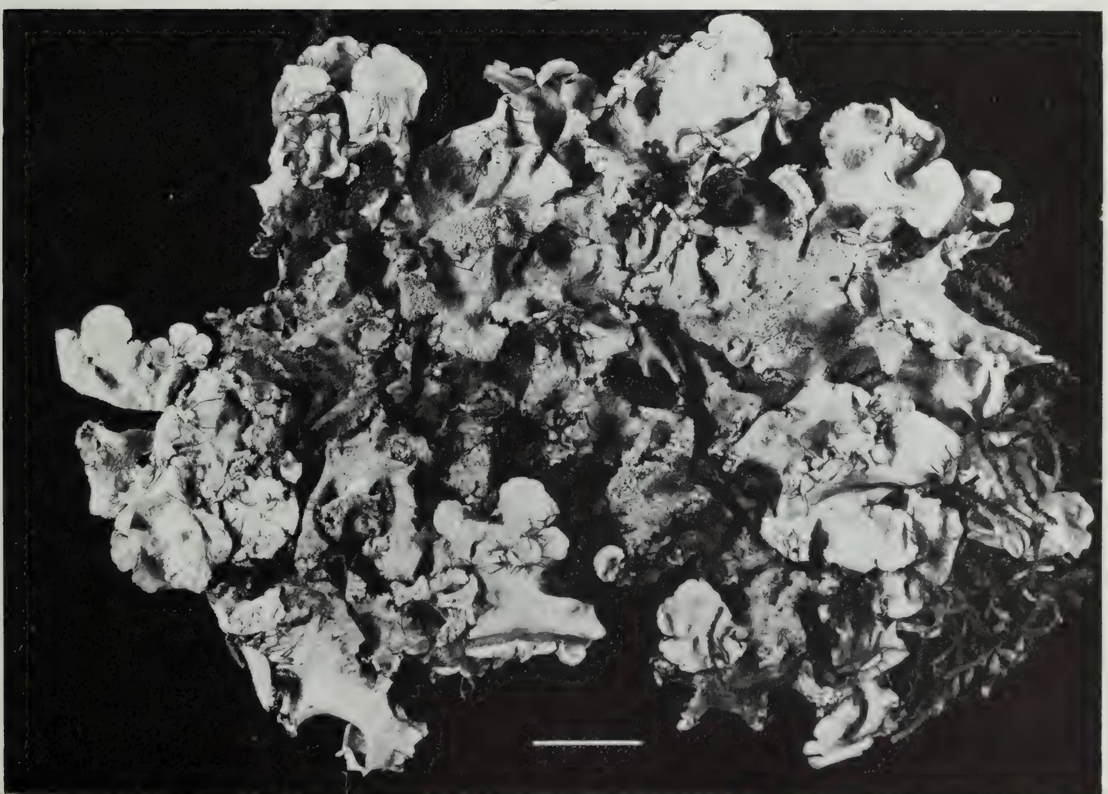

Fig. 6 *Parmelia cryptoxantha* des Abb., 4K 9/106 (O). Rule = 1 cm.

numerous, slender, up to 5 mm long. Upper cortex emaculate, fragile and flaking, sometimes with laminal cilia. Medulla with an unevenly distributed pale pink pigment. Underside smooth, shiny, black, with a brown marginal zone, rhizines sparse. Laminal pustules and open dactyls present, dissolving into corticate granules, soredia rare. Apothecia and pycnidia not found in East African material. (According to Hale (1965) the apothecia are imperforate with spores 24–28 × 10–12 μm.)

TLC: echinocarpic acid, protolichesterinic acid, pigment, atranorin.

Parmelia cryptoxantha is a species of shady, moist habitats in the lower montane forest. We have collected it between 1550 and 2100 m altitude in Kenya and Tanzania. Outside our area it is known from Madagascar and Natal (Hale, 1965).

East African records

Kenya. Central Province, Kirinyaga District, Mt Kenya, Irangi Forest Station, 5K 4/7; 2 km NW of Irangi Forest Station near River Ena, K 48/127. Eastern Province, Meru District, Mt Kenya, E side, on track to Themwe, 3K 15/111; Mt Kenya, NE slope, Chigora track, *Ryvarden* 11640 (O). Western Province, Kakamega District, Kakamega Forest, 0·5 km SW of forest station, 4K 9/106. **Tanzania.** Northern Province, Arusha District, Arusha National Park, near Ngurdoto Gate, T 6/109.

14. **Parmelia defecta** Hale **Fig. 7**

Contr. U.S. natn. Herb. **36** (5) : 244 (1965).—*Parmotrema defectum* (Hale) Hale, *Phytologia* **28** : 335 (1974). Type: Natal, District Bergville, Cathedral Peak area, Indumeni Forest, leg. *O. Almborn* 8934 (LD—holotype). [TLC: lecanoric acid, atranorin.]

Thallus saxicolous, coriaceous, adnate and strongly attached, pale grey, darker grey towards the centre. Lobes 0·5–1·5 cm broad, rounded or irregularly incised, eciliate, flat or with revolute margins. Upper cortex emaculate, shiny, finely cracked in older parts. Medulla white. Underside black, with a brown marginal zone, matt and rugose in the centre, smooth and shiny peripherally, rhizines sparse, fairly coarse. Soralia marginal and submarginal, with coarsely granular soredia. Apothecia unknown. Conidia filiform, 10–12 μm long.

TLC: lecanoric acid, atranorin.

Parmelia defecta has often been confused with saxicolous forms of *P. austrosinensis*, another eciliate, sorediate species with lecanoric acid. However, even when it grows on rock *P.*

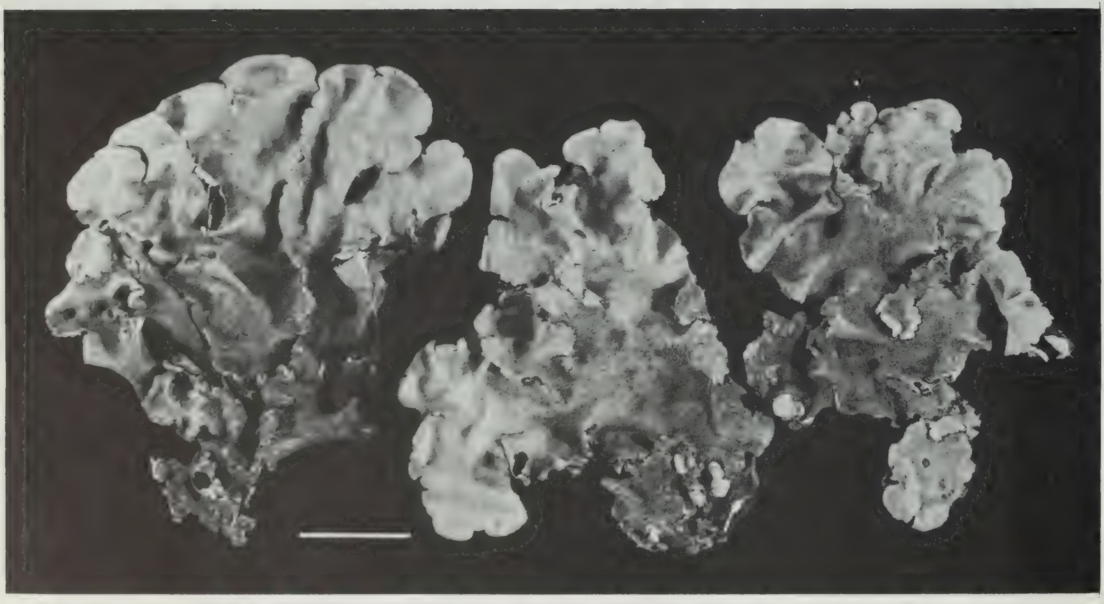

Fig. 7 *Parmelia defecta* Hale, 2K 9/107 (O). Rule = 1 cm.

austrosinensis has a loosely attached thallus and broader lobes with more or less ascending lobe margins. *Parmelia defecta* is believed to be the sorediate counterpart of *P. soyauxii.*

We have collected *P. defecta* in Kenya on dry, exposed rock between 1750 and 2100 m altitude, often accompanied by *P. pseudograyana.* A specimen from Entebbe, Uganda, coll. Proctor (K, US) was cited by Hale (1965, not seen). Outside our area the species has been reported from South Africa and Madagascar (Hale, 1965).

East African records

Kenya. Eastern Province, Machakos District, Lukenia, 30 km SE of Nairobi, 3K 1/117. Rift Valley Province, Uasin Gishu District, near Sergoi 27 km S of Chebiemit, 2K 9/107; Nakuru District, entrance of Masai Gorge, N of Lake Naivasha, K 30/104. Coast Province, Taita District, N of Mwanda summit, 2K 28/4, 101.

15. Parmelia dilatata Vainio

Acta Soc. Fauna Flora fenn. **7** (7) : 33 (1890).—*Parmotrema dilatatum* (Vainio) Hale, *Phytologia* **28** : 335 (1974). Type: Sitia, Minas Gerais, Brazil, *Vainio*, Lichenes Brasilienses Exs. 397 (BM—isotypes). [TLC: protocetraric acid, echinocarpic acid, traces of pigments, usnic acid, atranorin.]

Parmelia affluens Hale, *Phytologia* **22** : 141 (1971).—*Parmotrema affluens* (Hale) Hale, *Phytologia* **28** : 334 (1974). Type: Peru, Dept. San Martin, Tingo Maria, on tree on slope E of Tingo Maria in jungle, 625–1100 m, leg. *H. Allard* 20700 (US – holotype). [TLC: protocetraric acid, echinocarpic acid, pigments, undetermined substances, usnic acid, atranorin.]

Thallus corticolous, adnate, coriaceous, yellowish grey. Lobes 1–2 cm broad, eciliate, with entire or crenate margins. Upper side emaculate, becoming more or less irregularly cracked towards the centre. Medulla white or with an obscure yellowish pink pigment. Underside black, with a brown, naked marginal zone, rhizines sparse. Soralia marginal and linear on peripheral lobes and subcapitate on ascending lateral lobes, soredia granular. (Apothecia in a Brazilian specimen (S) laminal, up to 1 cm in diameter, disc imperforate, thalline exciple sorediate, spores 25–27 × 10–12 μm.) Pycnidia not seen.

TLC: protocetraric acid, echinocarpic acid, undetermined substances, pigments, usnic acid, atranorin.

The interpretation of *P. dilatata* has caused many problems, mainly owing to inadequate knowledge of its chemical properties. Hale (1965) considered that the type material of *P. dilatata* was an abnormal collection, being eciliate and containing a trace of usnic acid. He placed *P. robusta* Degel. and *P. gardneri* Dodge in synonymy with it, both sparsely ciliate species without usnic acid. Hale (1971*c*) described *P. affluens*, with protocetraric acid, atranorin, and various pigments and undetermined substances, one of which has since been identified as echinocarpic acid. In discussing his new species *Parmotrema progenes*, Hale (1977) pointed out that this was the fertile parent morph of *Parmelia dilatata*, with the same chemistry, namely atranorin, protocetraric acid, echinocarpic acid, and associated unknowns. He referred specimens with atranorin and protocetraric acid only, previously included in *P. dilatata*, to *P. robusta*.

One important detail in the chemistry of *P. affluens* and *P. progenes* has been largely overlooked, namely the presence of generous amounts of both atranorin and usnic acid in the cortex. As already mentioned above, Hale found usnic acid in the type specimen of *P. dilatata*. An undetermined spot of high Rf value in HEF and of a dark grey colour after treatment with dilute sulphuric acid and heat, reported for both *P. affluens* and *P progenes*, has proved to be usnic acid running more or less into other substances on the TLC plate.

The only difference between *P. dilatata* and *P. affluens* seems to be of a chemical nature; morphological characters, including spore size, are the same. However, the chemical difference appears to be quantitative rather than qualitative. There are, for example, traces of pigments in an isotype of *P. dilatata* in the BM, and the East African specimens showed presence of pigments by TLC, although the medulla appeared largely white under the low power binocular microscope. We regard *P. dilatata* as a species in which the medulla is inherently pigmented, but with considerable variation in the concentration of both the

pigments and other undetermined medullary substances, and we therefore place *P. affluens* in synonymy with it.

Parmelia dilatata appears to be rare in East Africa. It has been collected at one locality in Kenya and one in Tanzania, at 300 and 900 m altitude respectively, both within 60 km of the coast.

We have seen *P. dilatata*, pigmented chemotype, also from West Africa: Sierra Leone, Kasewe Forest Reserve, *Richards* R7185 L (BM). It is further known from South America and India (Hale, 1974*a*). The distribution of the unpigmented (or weakly pigmented) chemotype is uncertain owing to nomenclatural confusion, but the species is probably pantropical.

East African records

Kenya. Coast Province, Kwale District, Shimba Hills, Makadara Forest, *Santesson* 20889 (UPS). **Tanzania.** Tanga Province, Usambara Mts, Amani, in the surroundings of Forestry House, *Santesson* 23151 (UPS), *Moberg* 1472b (UPS).

16. Parmelia direagens Hale

Contr. U.S. natn. Herb. **36** (5) : 288 (1965).—*Parmotrema direagens* (Hale) Hale, *Phytologia* **28** : 335 (1974). Type: South Africa, near Kimberley, leg. *John Shaw* (BM—holotype). [TLC (Winnem 1974): psoromic acid, alectoronic acid, gyrophoric acid, atranorin.]

Thallus corticolous, loosely attached, pale grey to green-grey. Lobes 0·5–1·2 cm broad, rounded, entire or crenate, ciliate, cilia 1–3 mm long. Upper cortex emaculate, more or less cracked in older parts. Medulla white. Underside rugose, black, with a brown or rarely mottled marginal zone, rhizines fairly coarse, in unevenly distributed patches. Soralia marginal, linear. Apothecia unknown. Conidia sublageniform to rod-shaped, 7–8 μm long.

TLC: (1) psoromic acid, gyrophoric acid, alectoronic acid, atranorin; (2) psoromic acid, gyrophoric acid, atranorin; (3) psoromic acid, alectoronic acid, atranorin.

The psoromic acid is here mainly restricted to the soralia, which react PD+ sulphur yellow while the medulla usually is PD−. Alectoronic and gyrophoric acids are found in the medulla.

Parmelia direagens has been collected on trees in well lit sites in the lower montane forest between 1500 and 2600 m altitude. Outside our area it is known from South Africa (LD) and the Palni Hills in India (BM).

East African records

Ethiopia. See Winnem (1975). **Kenya.** Central Province, Nyeri District, Mt Kenya Safari Club, 4K 19/126; Nyeri District, Burguret River, 4K 27/107. Rift Valley Province, Laikipia District, Burguret, 4K 25/121. **Tanzania.** Northern Province, Arusha District, Mt Meru Crater, T 5/235. Eastern Province, Morogoro District, Uluguru Mountains, on W slope of Lupanga above Morogoro, *T. Pócs, P. Csontos & K. Csontos* 6067/A (herb. Pócs).

17. Parmelia durumae Krog & Swinscow sp. nov. **Fig. 8**

Thallus corticola, adnatus. Lobi profunde divisi, ad 1 cm lati, crenati vel irregulariter incisi, ciliis 1–3 (6) mm longis, superne laeves, emaculati, inferne ad centrum nigri, saepe zona marginale alba. Soralia isidiaque nulla. Apothecia marginalia vel submarginalia, stipitata, margine thallo ciliato, disco vulgo imperforato. Spori 22–26 × 12–15 μm. Conidia sublageniformia ad bacilliformia, 5–7 μm longa. Acidum alectoronicum, acidum α-collatolicum, et atranorinum continens.

Thallus corticolous, adnate or with more or less free lobe margins when growing on twigs, pale grey. Lobes deeply divided, up to 1 cm broad, crenate or irregularly incised, ciliate, cilia slender, 1–3 (6) mm long. Upper side smooth, emaculate except for vicinity of apothecia which is maculate, central parts often strongly rugose. Medulla white. Underside matt, rugose, black in the centre but soon turning dark brown, commonly with a wide, white or mottled marginal zone, rhizines short, sparse, restricted to the centre of the thallus. Soralia and isidia absent. Apothecia usually numerous, marginally and submarginally situated, stipitate, stipe sometimes formed by a convoluted lobe, thalline exciple smooth or ridged,

Fig. 8 *Parmelia durumae* Krog & Swinscow, holotype (O). Rule = 1 cm.

strongly maculate, thalline margin weakly dentate, ciliate, disc usually imperforate, becoming radially split with age, spores 22–26 × 12–15 μm. Pycnidia numerous, submarginal, conidia weakly sublageniform, 5–7 μm long.

TLC: alectoronic acid, α-collatolic acid, atranorin.

Type: Kenya. Coast Province, Kwale District, 2 km N of Gazi, 4° 22′ S, 39° 30′ E, at the edge of a mangrove, February 1974, Coll. *H. Krog & T. D. V. Swinscow* no. 3K 30/132, (O—holotype; BM, UPS—isotypes).

There are a number of alectoronic acid producing primary species with ciliate lobe margins and imperforate apothecia, but none of them seems to correspond to our species. Several of them, such as *P. argentina* Krempelh., *P. maclayana*, *P. subproboscidea* Lynge, *P. uberrima,* and *P. wainii* A. L. Sm., have smaller spores and differ also in various other characters. *Parmelia stenopteris* Kurok. differs chemically in that it produces fatty acids instead of α-collatolic acid; it has apothecia with a strongly dentate-lobulate thalline margin and a rugose exciple. *Parmelia subrugata* has thick-walled spores more than 30 μm long. *Parmelia pigmentifera* has similar ecology as *P. durumae* and resembles it morphologically; furthermore, both species give a strong UV+ reaction in the medulla. However, *P. pigmentifera* has a brown marginal zone on the underside and produces an ochraceous pigment and undetermined substances in the medulla.

Some of the Ugandan specimens have extremely long, dense cilia. They approach a species from Nigeria, issued as no. 31 in Almborn, Lichenes africani under the name *P. subrugata* Krempelh.

Parmelia durumae grows on twigs and branches at the edge of mangroves and in low coastal hills off the Indian Ocean, from sea level to *c.* 300 m altitude, and has also been collected in Uganda at about 1100 m.

East African records

Kenya. Coast Province, Kwale District, 2 km N of Gazi, K 44/112, 3K 30/132 (type collection), Shimba Hills, 25 km SW of Mombasa, Kivumoni Forest, K 41/1, 104, Tschamtei in Duruma, January

1877, *Hildebrandt* 2333 (M); Kilifi District, Mida Creek, 3K 29/113. **Uganda.** Busoga District, Mutai, December 1950, *Wood* (BM). Masaka District, Bukoto County, Jubiya Forest, 3U 32/107, *Lye* L 604 (herb. Lye). Toro District, Bwamba, Ituri Forest, *Pentecost* RE 240 (BM). N Mengo District, 7 miles N of Nakasongola, 1918, *Langdale-Brown* (EA).

18. Parmelia eciliata (Nyl.) Nyl.

in Fournier, *Mex. Pl.* **3** : (1872).—*Parmelia crinita* var. *eciliata* Nyl., *Flora, Jena* **52** : 291 (1869).—*Parmotrema eciliatum* (Nyl.) Hale, *Phytologia* **28** : 336 (1974). Type: Mexico, Orizaba, *E. Bourgeau* s.n. (H–NYL 35295—holotype). [TLC: stictic acid, constictic acid, atranorin.]

Parmelia eurycarpa Steiner & Zahlbr., *Bot. Jb.* **60** : 530 (1926). Deutsch Ostafrica, Ost-Usambara, im Regenwald auf Baumstämmen b. Amani, 800 m, leg. *Brunnthaler* (W—holotype). [TLC: stictic acid, constictic acid, atranorin.]

Thallus corticolous, loosely attached, pale grey. Lobes 0·5–0·8 cm broad, crenate or irregularly incised, ciliate, cilia 1–2·5 mm long. Upper cortex emaculate, rugose towards the centre. Medulla white. Underside smooth, black, with a brown marginal zone, rhizines abundant. Soralia and isidia absent. Apothecia numerous, stipitate, thalline exciple more or less rugose, disc imperforate, spores 26–30 × 18–20 μm, thick-walled. Conidia rod-shaped. *c.*8 μm long.

TLC: stictic acid, constictic acid, atranorin.

Parmelia eciliata is rare in East Africa. It has been collected in Tanzania in the lower montane forest between 800 and 1200 m altitude. According to Hale (1965) it is widespread in the West Indies and in Central and South America; it was reported from Japan and Taiwan by Kurokawa (1968) and it is also known from South Africa.

East African records
Tanzania. Eastern Province, Morogoro District, Mindu Forest Reserve, 4 May 1978, *Dahl* (O). Tanga Province, Tanga District, East Usambara Mountains, Amani Forest Reserve, *T. & S. Pócs* 6086/T (herb. Pócs), East Usambara by Amani, *Brunnthaler* (W—holotype of *P. eurycarpa*).

19. Parmelia erubescens Stirton

Scott. Nat. **4** : 201 (1877–78). Type: Queensland, Brisbane, *F. M. Bailey* 11 (BM—holotype). [TLC (Winnem 1974): salazinic acid, atranorin.]

Parmelia virens Müll. Arg., *Flora, Jena* **69** : 255 (1886). Type: Queensland, Toowoomba, 1882, *Hartmann* (G—holotype). [TLC: salazinic acid, atranorin (+).]

Thallus somewhat coriaceous, corticolous, loosely attached, pale grey-green. Lobes 0·5–1 cm broad, rounded, crenate, ciliate, cilia 0·8–1·5 mm long. Upper side in part maculate, rugose and cracked towards the centre. Underside black, with a brown marginal zone, rhizines dimorphous, here and there reaching almost to the margins. Soralia and isidia absent. Only immature apothecia and pycnidia found in the East African specimen. (The type of *P. virens* has spores 10–12 × 8–10 μm, and filiform conidia 10–12 (14) μm long.)

TLC: salazinic acid, norlobaridone, atranorin (+).

Hale (1965) regarded *P. erubescens* as conspecific with *P. subcaperata* Krempelh., a species which has proved to contain considerable amounts of usnic acid in the cortex in addition to atranorin. We believe that *P. subcaperata* is distinct from *P. erubescens*, and that it is closely related to the isidiate species *Parmotrema neotropicum* Kurok.

The East African specimen was small and immature, and did not show the strongly maculate upper side which is so typical for this species group. However, features of the underside, the presence of some maculate areas, and chemical properties leave little doubt about its taxonomic position.

Parmelia recipienda Nyl., with norlobaridone, is probably conspecific with *P. erubescens* (Table 13). For further discussion, see under 'Circumscription of the species'.

Interpreted in its wide sense, *P. erubescens* is known from Australia and Brazil, and from one locality in Kenya where it grew in a well lit site at 1400 m altitude.

East African record
Kenya. Eastern Province, Machakos District, Ol Doinyo Sapuk, 20 km SE of Thika, 2 K 1/108.

20. Parmelia euneta Stirton **Fig. 9**

Scott. Nat. **4** : 298 (1877–78).—*Parmotrema eunetum* (Stirton) Hale, *Phytologia* **28** : 336 (1974). Type: Africa (tropical), Victoria, *Thomson* s.n. (BM—holotype). [TLC: gyrophoric acid, atranorin.]
Parmelia composita Hale, *Phytologia* **23** : 243 (1972).—*Parmotrema compositum* (Hale) Hale, *Phytologia* **28** : 335 (1974). Type: Tanzania, Arusha Province, Mt Meru, E slope, *c.* 2 km N of Kitoto Camp, alt. 2400 m, *Santesson* 22985a (UPS—holotype, BM—isotype). [TLC: gyrophoric acid, norstictic acid, atranorin.]
Parmelia spilota Hale, *Phytologia* **27** : 3 (1973).—*Parmotrema spilotum* (Hale) Hale, *Phytologia* **28** : 339 (1974). Type: Tanzania, Horombo Hut, Kilimanjaro, 3750 m, 9 January 1969, *H. D. Griffin* (O—isotype). [TLC: norlobaridone, norstictic acid, atranorin.]

Thallus corticolous or saxicolous, membranaceous to somewhat coriaceous, loosely attached, pale grey to grey-green. Lobes (0·5) 1–2 (3) cm broad, entire, crenate, or irregularly incised, ciliate, cilia 1–3 (4) mm long. Upper side strongly maculate, cracked in older parts, here and there with discoloured areas. Medulla white, with occasional patches of an ochraceous, K+ purple pigment (skyrin) near the lower cortex. Underside black, with a brown, naked marginal zone, sometimes white mottled underneath the apothecia, rhizines coarse or slender, often branched, sparse to abundant, unevenly distributed. Soralia and isidia absent. Apothecia submarginal, stipitate on more or less swollen stipes, thalline exciple rugose, thalline margin crenate-dentate, disc up to 2 cm in diameter, commonly perforate but sometimes imperforate and radially split, spores 20–26 (30) × 12–15 (17) μm, relatively thick-walled. Conidia filiform, 12–16 (20) μm long.

TLC: (1) gyrophoric acid, ± norstictic acid, atranorin; (2) norlobaridone, ± norstictic acid, atranorin; (3) gyrophoric acid, norlobaridone, ± norstictic acid, atranorin; (4) norstictic acid, atranorin (rare).

Hale (1965) considered *P. euneta* to be a species with a normally ciliate thalline exciple, a faintly to distinctly maculate upper cortex, and gyrophoric acid in the medulla. Later, Hale (1972) described the new species *P. composita*, containing gyrophoric and norstictic acids. It, too, had a maculate upper cortex, and the spores were 22–24 μm, that is, in the same size

Fig. 9 *Parmelia euneta* Stirton, E 30/21 (○). Rule = 1 cm.

range as those reported for *P. euneta.* Winnem (1975), who had not seen the type of *P. euneta*, found no gyrophoric acid containing specimens with a ciliate thalline exciple in her Ethiopian material and concluded that the species was not represented in her collections. On the other hand, she found no morphological differences between specimens with only gyrophoric acid and specimens with both gyrophoric and norstictic acids, and consequently included both chemotypes in *P. composita*, regarding the norstictic acid as an accessory substance.

The type of *P. euneta*, in the BM, is a small scrap about 2 × 3 cm, but it shows the most important characters of the species, such as marginal cilia, an eciliate thalline exciple, a strongly maculate upper cortex, fairly thick-walled spores 23–26 × 13–15 μm and filiform conidia 12–15 μm long, agreeing fully with *P. composita.* We follow Winnem (1975) in regarding norstictic acid as an accessory substance and reduce *P. composita* to synonymy with *P. euneta*.

In 1973 Hale described *P. spilota*, a species with norlobaridone and norstictic acid in the medulla and a maculate upper cortex; apothecia were unknown at the time. Winnem (1975) referred Ethiopian specimens with only norlobaridone to the same species, again regarding norstictic acid as an accessory substance. She found that the species had perforate apothecia and spores 20–25 μm long. In Kenya and Uganda we have found morphologically similar specimens with a combination of gyrophoric acid and norlobaridone, still with norstictic acid as an accessory substance. We consider that this chemotype connects *P. spilota* with *P. euneta*, and regard the two species as synonymous (Table 11). For further discussion, see under 'Circumscription of the species'.

One of our specimens, from Tanzania (T 16/118), had only norstictic acid but corresponded to *P. euneta* in all other characters. It had spores 25–28 × 12–15 μm, and filiform conidia 12–14 μm long.

Parmelia euneta is a mainly corticolous species of inselbergs and montane forests, extending into the low alpine zone where it often grows on rock. It has been collected between 1600 and 3750 m altitude. Outside our area the species has been reported from Sierra Leone, Angola, Zaïre, Sri Lanka, and Haiti (Hale, 1965). However, these records need verification, since Hale interpreted the species in a wide sense, including, for example, specimens with a ciliate thalline margin of the apothecia and weakly developed maculae.

Selected East African specimens
Ethiopia. Presso la chiesa di Sciaurá Mariám Alefa, *Pichi-Sermolli* 70 (BP). For further records, see Winnem (1975) under *P. composita* and *P. spilota.* **Kenya.** Rift Valley Province, Uasin Gishu District, 5 km NW of Timboroa Summit, 2K 19/110; Laikipia District, Burguret, 4K 25/124; Trans Nzoia District, Mt Elgon crater, at Maji ya Moto (hot springs), *Hedberg* 949, 950 m (UPS); Kajiado District, Ngong Hills, K 45/18, 119. Central Province, Nyeri District, Burguret River, 4K 27/108, Mt Kenya, W side, Naro Moru track, K 34/108; Kirinyaga District, Mt Kenya, S slope, 2 km NW of Irangi Forest Station near River Ena, K 48/109. Eastern Province, Meru District, Mt Kenya, E side, at Themwe, 3K 16/112, Mt Kenya, N side, Sirimon track, 4K 24/116. **Tanzania.** Northern Province, Arusha District, Mt Meru Crater, T 5/113; Moshi District, Kilimanjaro, Horombo Hut, *Griffin* (O—isotype of *P. spilota*); Masai District, Ngorongoro Crater, on the rim, near the post office at Ngorongoro, *Sipman* 6381A (herb. Sipman). Southern Highlands Province, Mbeya District, between Kimondo and Kikondo, 9 May 1978, *Dahl* (O). **Uganda.** Bugisu District, N Bugisu County, by Sasa Hut on Mt Elgon, 2U 44/62.

21. Parmelia eurysaca Hue

Nouv. Archs Mus. Hist. nat., Paris IV, **1** : 194 (1899).—*Parmotrema eurysacum* (Hue) Hale, *Phytologia* **28** : 336 (1974). Type: Mexico, 1865–66, *Bourgeau* (PC—holotype). [TLC: not tested.]

Thallus corticolous, membranaceous, loosely attached, pale grey-green. Lobes 0·8–1·2 cm broad, rounded, entire or crenate peripherally, laciniate-lobulate towards the centre of the thallus, ciliate, cilia slender, simple or bifurcate, 2–3 mm long. Upper side emaculate. Medulla white. Underside black, with a brown, shiny, naked marginal zone, rhizines slender, simple or bifurcate, unevenly distributed. Soralia and isidia absent. No apothecia or pycnidia

seen in the East African specimen. (Mexican specimens in O have stipitate apothecia with perforate discs, and spores 12–16 × 8–10 μm. The conidia are rod-shaped to shortly filiform, 8–10 μm long.)

TLC: salazinic acid, atranorin.

It is with considerable hesitation that we identify our sterile specimen as *P. eurysaca*, but the laciniate central lobes and the content of salazinic acid point to that species.

The specimen grew in a rain forest in the Uluguru Mountains in Tanzania between 1300 and 1800 m altitude. The species has its main area in the southern United States and Mexico (Hale, 1965).

East African record

Tanzania. Eastern Province, Morogoro District, rain forest above Morningside in the Uluguru Mountains, 6 May 1978, *Dahl* (O).

22. Parmelia gardneri Dodge **Fig. 10**

Ann. Mo. bot. Gdn **46** : 179 (1959). Type: Brazil, *Gardner* (FH—holotype). [TLC: protocetraric acid, atranorin.]

Thallus corticolous, coriaceous, adnate or loosely attached, pale grey to green-grey. Lobes 0·8–1·5 (2) cm broad, crenate, irregularly incised, or sublaciniate, eciliate or rarely sparingly ciliate, cilia 0·2–0·5 mm long, lobe margins more or less ascending. Upper side emaculate or faintly maculate. Medulla white. Underside black, with a broad, brown or mottled, naked marginal zone, rhizines short, sparse. Soralia marginal and submarginal, forming complex, raised sorediate structures on narrow lateral lobes, soredia granular. Apothecia laminal, subsessile, thalline exciple sorediate, disc usually imperforate, spores 18–22 (24) × 8–10 (11) μm. Conidia sublageniform, 6–7 μm long.

TLC: protocetraric acid, ± fatty acids, atranorin.

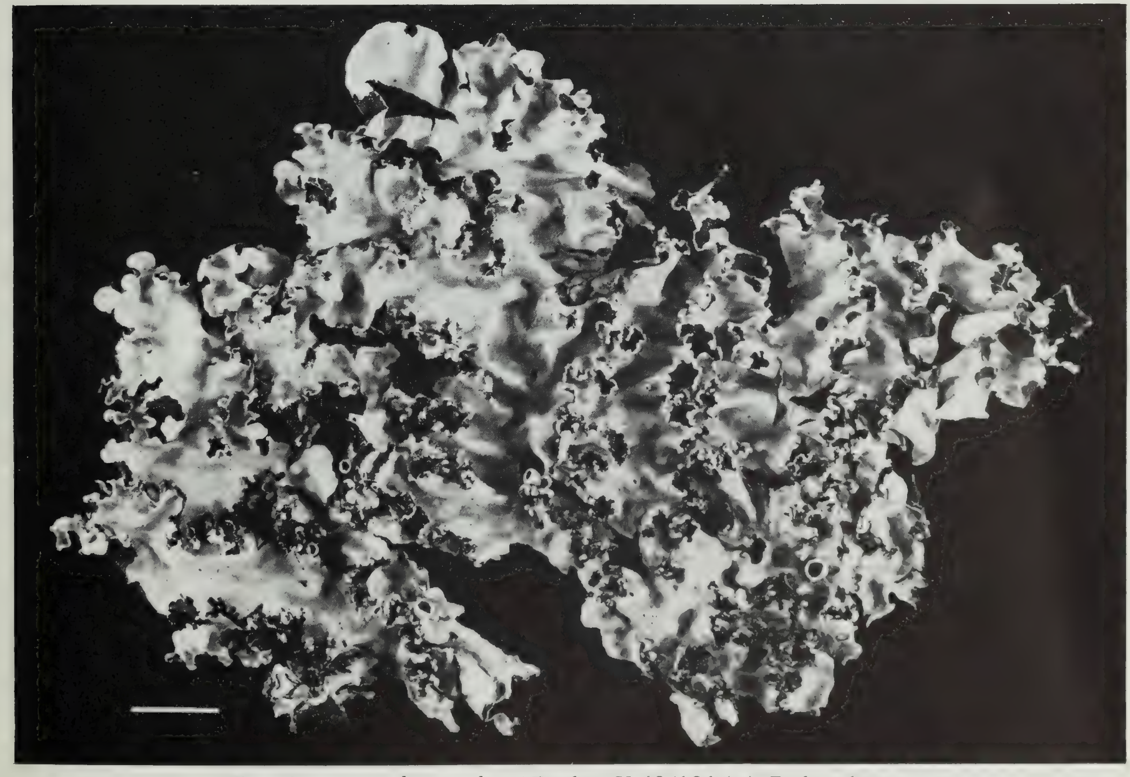

Fig. 10 *Parmelia gardneri* Dodge, K 43/101 (O). Rule = 1 cm.

We regard *P. gardneri* as the sorediate counterpart of *P. zollingeri.* It has often been determined as *P. dilatata*, but differs in the smaller spores, lack of usnic acid in the cortex, and a less complicated medullary chemistry. From *P. robusta* Degel., another sorediate species with protocetraric acid, it differs in a more coriaceous thallus and in ecological traits. (In the Canary Islands, for example, *P. robusta* is a species of the laurel forest at about 800–1200 m altitude. If it occurred in our area it would most certainly grow in the upper montane forest. It appears to have a mainly Atlantic–Lusitanian distribution, and there are no reliable records of it from continental Africa.)

Parmelia gardneri grows on twigs, branches, and tree boles, and can, when well developed, reach a diameter of 30 cm but is usually smaller. It grows in mangroves and in the low coastal hills off the Indian Ocean, and occurs farther inland at around 1000–2000 m altitude. All collecting sites were fairly dry and well lit. The species is believed to be more or less pantropical.

East African records

Kenya. Eastern Province, Machakos District, lava flow 5 km NW of Kibwezi, K 20/145, 3K 23/126; Meru District, near Chogoria, 3K 7/110, 3K 9/102, Mt Kenya, E side, at Themwe, 3K 16/197. Coast Province, Kwale District, Kwale, Forestry Station, *Santesson* 20802a pro parte (UPS), Shimba Hills, 25 km SW of Mombasa, Kivumoni Forest, K 41/101, K 42/101, Pengo Hill, *Santesson* 20896 (UPS), Makadara Forest, K 43/3, 2 km N of Gazi, K 44/31, 105, 3K 30/33, 146; Kilifi District, Gedi ruins, 3K 25/105, Mida Creek, edge of mangrove, 3K 29/118. **Tanzania.** Lake Province, Mwanza District, Massanza, *Sitari* 609 (TUR). Northern Province, Moshi District, by track from Marangu to Mandara Hut, *Burnet* 161 (BM). Eastern Province, Morogoro District, Kitulangala Forest Reserve, 6 May 1978, *Dahl* (O). Tanga Province, Lushoto District, East Usambara Mts, Amani Forest Reserve, *T. & S. Pócs* 6086/O (herb. Pócs), Amani, surroundings of Forestry House, *Moberg* 1471a (UPS), Amani, road towards SW, *Santesson* 23406 (UPS). **Uganda.** W Mengo District, Busiro County, Entebbe Botanical Garden, 3U 5/1. Masaka District, Bukoto County, near Kasaka in Jubiya Forest, *Lye* L 606 (herb. Lye).

23. **Parmelia grayana** Hue

Nouv. Archs Mus. Hist. nat., Paris IV, **1** : 184 (1899).—*Parmotrema grayanum* (Hue) Hale, *Phytologia* **28** : 336 (1974). Type: India, in Coonoor in montibus Nilgherrensibus, 1893, leg. *Gray* (PC—holotype). [TLC: not tested.]

Thallus saxicolous, firmly attached, pale grey. Lobes up to 0·7 cm broad, rounded, margins ascending, crenate, ciliate, cilia 0·5–1·5 mm long. Upper side emaculate. Medulla white. Underside black, with a brown, naked marginal zone, rhizines coarse. Soralia marginal and submarginal, soredia often with a grey-brown tinge. Apothecia absent in East African material. (According to the protologue, the spores are 15–16 × 7–8 μm.) Conidia sublageniform to rod-shaped, 8–10 μm long.

TLC: protolichesterinic acid, atranorin.

Parmelia grayana appears to be rare in our area; it has been collected twice in Uganda on exposed rock at 1160 and 1500 m altitude. It is also known from South Africa, the Canary Islands, India, and Japan (Hale, 1965), Australia (Kurokawa, 1969), and Arizona (BM).

East African records

Uganda. Masaka District, Bukoto County, SE of Lake Kayanja, *Lye* L 710 (herb. Lye). Ankole District, Igara County, south side of Lubare Ridge, 11 km S of Rubirizi, 2U 15/1.

24. **Parmelia hababiana** Gyelnik

Reprium nov. Spec. Regni veg. **29** : 288. (1931).—*Parmotrema hababianum* (Gyelnik) Hale, *Phytologia* **28** : 336 (1974). Based on *Parmelia abessinica* var. *sorediosa* Müll. Arg., *Flora, Jena* **68** : 501 (1885). Type: Abessinia, prope Habab, *Hildebrandt* 310 pp. (G—lectotype). [TLC: protolichesterinic acid, atranorin.]

Thallus mainly corticolous, membranaceous to coriaceous, more or less adnate but with ascending lobe margins, pale grey to grey-green. Lobes 0·5–1·5 cm broad, ciliate, cilia

0·2–2·5 (4) mm long. Upper cortex faintly to rarely distinctly maculate, rugose towards the centre. Medulla white. Underside smooth or rugose, black, with a brown, mottled, or white marginal zone, rhizines in scattered groups or more or less evenly distributed. Soralia marginal and submarginal. Apothecia with entire or sorediate thalline margin, disc perforate, spores 13–17 (20) × 8–10 μm. Conidia weakly sublageniform, 6–8 μm long.

TLC: (1) norlobaridone, ± loxodin, protolichesterinic acid, atranorin; (2) norlobaridone, ± loxodin, atranorin; (3) protolichesterinic acid, atranorin.

In dry, well lit sites *P. hababiana* has a rather coriaceous, grey thallus with short marginal cilia, and a rugose under side with a mottled or white marginal zone. However, when it grows in more shady habitats, the thallus may be membranaceous, grey-green, with fairly long marginal cilia, and have a smooth underside with a brown marginal zone. There is no correlation between morphological and chemical variation.

Parmelia hababiana is one of the commonest lichens of dry, well lit upland habitats. It has been collected between 800 and 2650 m altitude, but is most common between 1500 and 2000 m. The species is particularly widespread in Africa, and is, according to Hale (1965), known also from India and the Americas.

Selected East African records

Ethiopia. See Winnem (1975). **Kenya.** Central Province, Kiambu District, escarpment E of Rift Valley, 35 km NW of Nairobi, K 15/106; Nyeri District, Mt Kenya, W side, by Naro Moru track, K 33/104; Kirinyaga District, Mt Kenya, S side, 2 km NW of Irangi Forest Station near River Ena, K 48/137; Embu District, Embu, by Izaak Walton Inn, 3K 6/103. Eastern Province, Machakos District, Kilima Kiu, 70 km SE of Nairobi, K 54/21b; Meru District, between Chogoria and South Mara River, 3K 11/103. Rift Valley Province, Elgeyo Marakwet District, Sogotio Forest 8 km N of Chebiemit, 2K 10/104; Nakuru District, cliff E of road by Lake Elmenteita, 2K 20/115; Kericho District, Kericho Tea Hotel, 4K 7/110; Samburu District, WSW slope of Warges, 4K 3/114. Western Province, Kakamega District, Kakamega Forest, 0·5 km SW of forest station, 4K 9/113. Coast Province, Taita District, above Wundanyi, 2K 25/101. **Tanzania.** Northern Province, Arusha District, Arusha National Park, Juniper Hill, T 3/115; Mbulu District, Babati, *Sitari* 551–a (TUR). **Uganda.** Mubende District, Buwekula County, Mubende Hill, 3U 12/5. Kigezi District, Rubanda County, 8 km W of Hamurwa, 3U 47/2. Toro District, Busongora County, Kyabikere, 7 km N of Bwera, 2U 5/5.

25. **Parmelia hanningtoniana** Müll. Arg. **Fig. 11**

Flora, Jena **73** : 339 (1890).—*Parmotrema hanningtonianum* (Müll. Arg.) Hale, *Phytologia* **28** : 336 (1974). Type: Trop. Afric. (or.) 2–7° lat. austr. *Rev. J. Hannington* (G—holotype, BM—isotype). [TLC: gyrophoric acid, fatty acids, atranorin.]

Thallus corticolous, loosely attached, pale green-grey. Lobes up to 1 cm broad, ciliate, cilia 1–3 mm long. Upper side smooth to wrinkled, distinctly maculate. Medulla white. Underside dark brown, strongly rugose, with scattered, agglomerated, black granules interspersed with groups of coarse, black rhizines. Soralia and isidia absent. Apothecia marginal and submarginal, urceolate, up to 15 mm in diameter, disc perforate or imperforate, sometimes radially split, thalline exciple covered with coarse, isidioid protuberances which frequently bear cilia, spores 18–20 × 8–10 μm. Conidia sublageniform, 5–7 μm long.

TLC: gyrophoric acid, fatty acids, atranorin.

Hale (1965) believed that *P. hanningtoniana* was restricted to the savannas of West Africa, but the type specimen probably came from Tanzania, where Hannington collected extensively in central parts of the country. The specimen AB 1389–g, cited below, grew just south of Hannington's area. Outside East Africa the species is known from Angola (BM, FI) and Zaïre (Hale, 1965). There is one specimen from Brazil, coll. Richard, in the BM, and another specimen from the same country mixed with the type specimen of *P. subcaperata* Krempelh. in M. These are the first records of the species from South America. All known localities lie between the equator and *c.* 20° S.

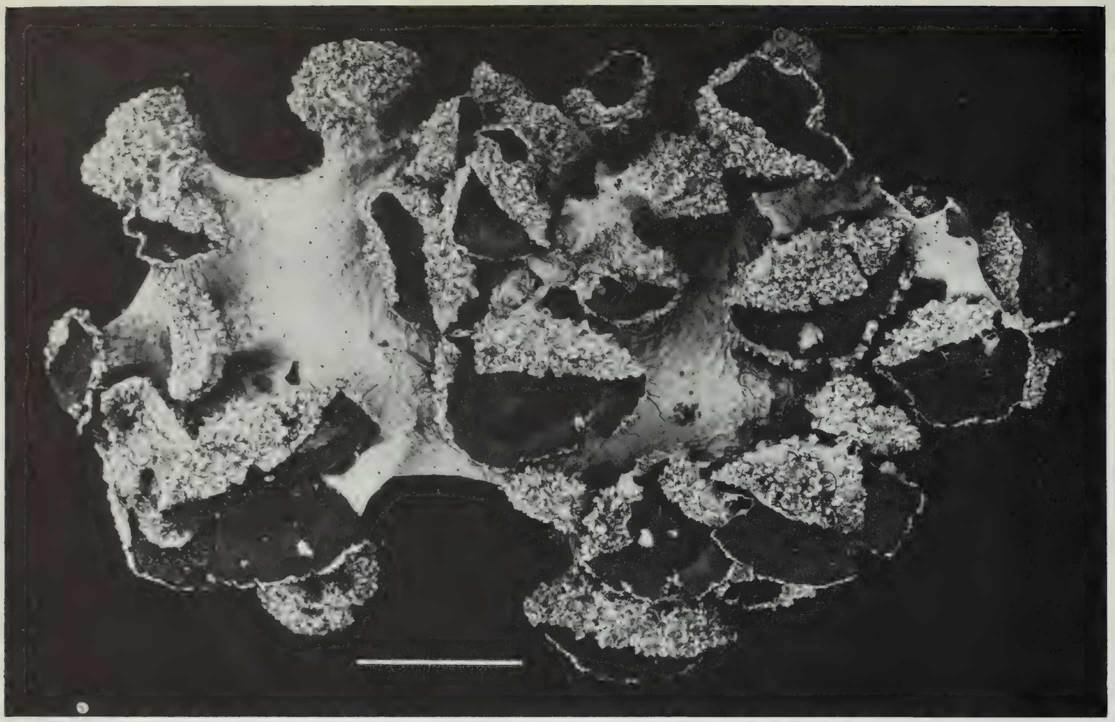

Fig. 11 *Parmelia hanningtoniana* Müll. Arg., *Bjørnstad* AB 1389-g (O). Rule = 1 cm.

East African records

Tanzania. Trop. Afric. or., 2–7° S, *Hannington* s.n. (G, BM—type collection). Southern Highlands Province, Iringa District, 50 km S of Iringa along road to Mbeya, 1700 m alt., *Bjørnstad* AB 1389–g (O).

26. Parmelia hololoba Hale **Fig. 12**

Contr. U.S. natn. Herb. **36** (5) : 293 (1965).—*Parmotrema hololobum* (Hale) Hale, *Phytologia* **28** : 336 (1974). Type: Uganda, Entebbe, 3 March 1959, *Proctor* (packet A) (BM—holotype). [TLC: lecanoric acid, atranorin.]

Thallus corticolous, loosely attached, pale grey. Lobes up to 2 cm broad, rounded, entire or crenate, flat or revolute, ciliate, cilia (0·5) 2–4 mm long. Upper side emaculate or faintly maculate. Medulla white. Underside black, with a brown or mottled marginal zone, rhizines short, unevenly distributed. Soralia and isidia absent. Apothecia marginal to submarginal, stipitate, up to 3 cm in diameter, thalline exciple smooth or rugose, strongly maculate, disc perforate, often eccentrically orientated in relation to the stipe, spores (12) 15–18 (20) × (6) 8–10 μm. Conidia filiform, 12–16 μm.

TLC: lecanoric acid, atranorin.

Parmelia hololoba is particularly well developed in habitats close to the sea coast. It is then emaculate, has well developed cilia, a smooth thalline exciple, and a mainly brown marginal zone on the under side. In inland sites the cilia often become short and stunted, the cortex more or less maculate, the thalline exciple rugose, and the underside white mottled towards the margins, in short, it becomes indistinguishable from *P. andina* except for the presence of rudimentary cilia. We consider this morphological convergence to be environmentally induced, and rely on the presence or absence of cilia for the separation of the two species.

As here delimited, *P. hololoba* grows at sea level by the Indian Ocean and in well lit upland

habitats more or less influenced by mist, between 1000 and 1800 m altitude. It was previously known only from the type locality.

East African records

Kenya. Coast Province, Kwale District, 2 km N of Gazi, K 44/25, 105, 3K 30/21, 115; Kilifi District, Mida Creek, 3K 29/122, Gedi ruins, 3K 25/106. Eastern Province, Machakos District, Ol Doinyo Sapuk, 20 km SE of Thika, 2K 1/103. Rift Valley Province, Kajiado District, Chyulu Hills, K 39/5A, 103; Samburu District, WSW slope of Warges, 4K 3/105; Laikipia District, Burguret, 4K 25/131. **Tanzania.** Northern Province, Arusha District, Arusha National Park, Kusare Forest, T 2/126. Tanga Province, Lushoto District, Usambara Mts, Magamba *c.* 4 km N of Lushoto, *Ryvarden* 10912 (O), near Amani, *T. & S. Pócs* 6087/A (herb. Pócs). Eastern Province, Morogoro District, N Uluguru Mts., gorge of Mt Kinazi above Morogoro, *Pócs* 6289/AY (herb. Pócs). **Uganda.** W Mengo District, Busiro County, Entebbe, *Proctor* (BM—type collection).

27. Parmelia indoafra Krog & Swinscow nom. nov. — Fig. 13

Parmotrema indicum Hale, *Mycotaxon* **5** : 436 (1977), non *Parmelia indica* Sprengel (1827). Type: India, Tamil Nadu, Kodaikanal, forest below Silver Cascade, on rocks in stream, *Hale & Patwardhan* 43874 (US—holotype, BM—isotype). [TLC: gyrophoric acid, norlobaridone, atranorin.]

Thallus corticolous (or saxicolous), coriaceous, pale grey. Lobes 1–2 cm broad, crenate, ciliate, cilia 0·5–2 (3) mm long. Upper cortex emaculate, rugose and irregularly cracked towards the centre, sometimes pruinose peripherally. Medulla white. Underside smooth to rugose, black, with a brown or mottled marginal zone, rhizines numerous, some of them fairly coarse, occasionally branched. Soralia marginal on some main lobes and on numerous narrow, ascending lateral lobes, here and there spreading submarginally. Apothecia unknown. Conidia shortly filiform, 10–12 (14) μm long.

TLC: gyrophoric acid, norlobaridone, atranorin.

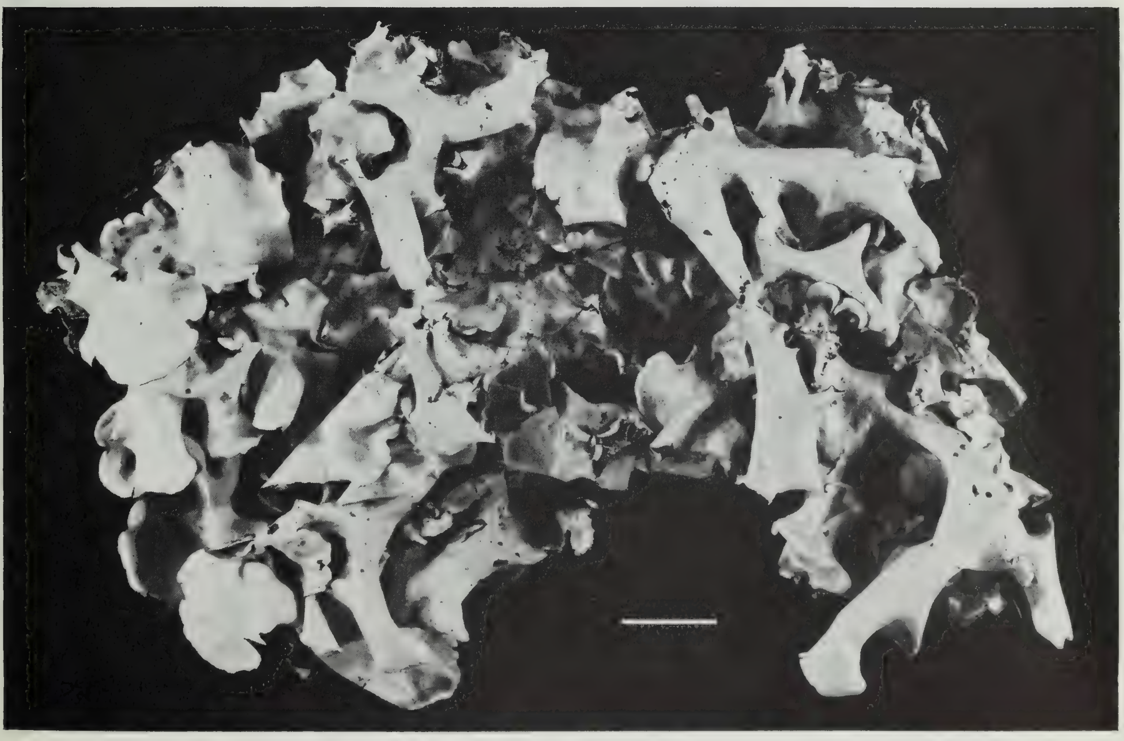

Fig. 12 *Parmelia hololoba* Hale, *Ryvarden* 10912 (O). Rule = 1 cm.

The species was recently described from India (Hale, 1977), and it is here reported for the first time from Africa. The Ethiopian specimens cited below were included in *P. balensis* (=*P. subschimperi*) by Winnem (1975). The two species have the same chemical properties, but *P. subschimperi* has a strongly maculate upper cortex and different ecological requirements.

Parmelia indoafra is in East Africa an upland species of fairly dry and well lit sites with local influence of mist. It has mainly been collected between 1450 and 1900 m altitude, with the exception of one collection from 2600 m.

East African records

Ethiopia. Sidamo Province, 10 km NW of Wadera, *Winnem* 595/8, 9 (O); 12 km S of Kebre Mengist, E 13/14; Yirga Alem, Sidamo Provincial Hospital, E 20/10. **Kenya.** Eastern Province, Marsabit District, Mt Marsabit, vicinity of Lake Paradise, 4K 6/129. **Tanzania.** Northern Province, Arusha District, Mt Meru Crater, T 5/161, Arusha National Park, Kusare Forest, T 2/101, near Ngurdoto gate, T 6/108, 111. **Uganda.** Toro District, Burahya County, 1 km N of Fort Portal, *Pentecost* RE 23 (BM).

28. Parmelia inexpectata des Abb.

Bull. Inst. fr. Afr. noire A, **20** : 16 (1958).—*Parmotrema inexpectatum* (des Abb.) Hale, *Phytologia* **28** : 337 (1974). Type: Côte d'Ivoire (Afr. Occ.), in Monte Tonkoui, prope Man, ad truncum Cinchonae, 1150 m, 16 October 1951, *des Abbayes* (US—isotype). [TLC: the lividic acid complex, atranorin.]

Parmelia paradoxa Hale, *Phytologia* **27** : 1 (1973).—*Parmotrema paradoxum* (Hale) Hale, *Phytologia* **28** : 338 (1974). Type: Uganda, Masaka District, Bukoto County, northern edge of Malabigambo Forest, 1100 m, December 1971, coll. *T. D. V. Swinscow* no. 3U 25/4B (BM—holotype). [TLC: the lividic acid complex, atranorin.]

Thallus corticolous, loosely attached, pale grey. Lobes rounded, up to 1 cm broad, abundantly ciliate, cilia 2–4 mm long. Upper side smooth, emaculate, more or less rugose towards the centre of the thallus. Medulla white. Underside black, with a broad, brown,

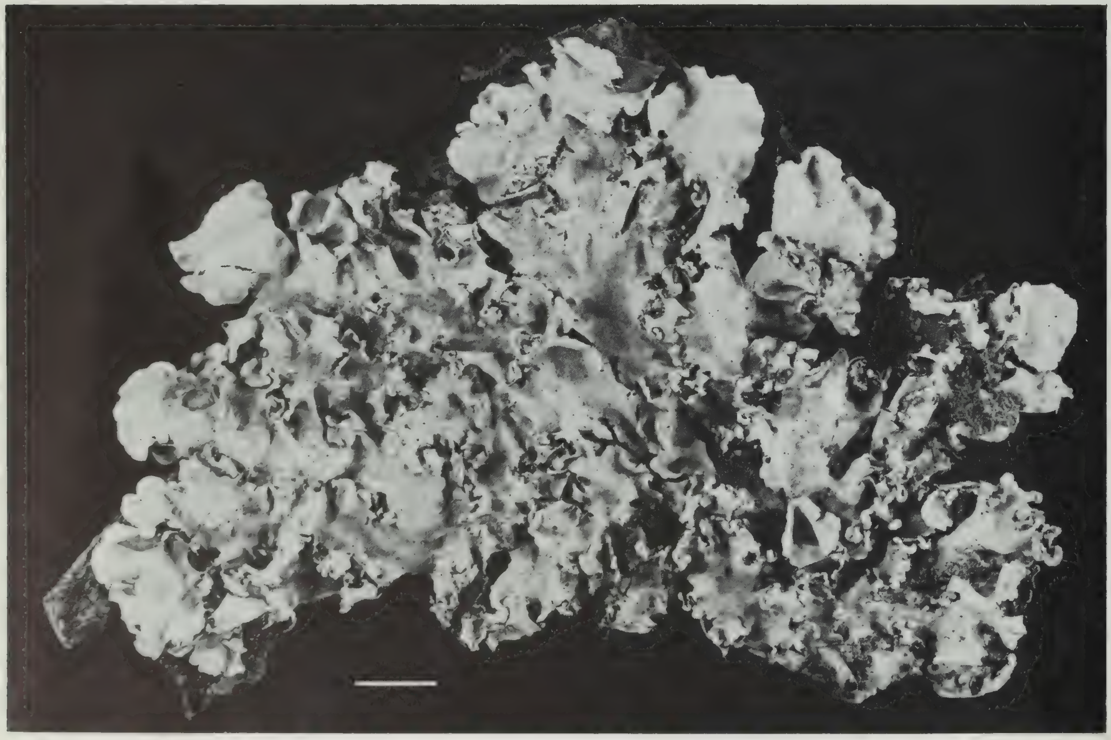

Fig. 13 *Parmelia indoafra* Krog & Swinscow, T 6/111 (O). Rule = 1 cm.

naked marginal zone, rhizines sparse. Soralia and isidia absent. Apothecia submarginal, stipitate, thalline exciple and stipe strongly maculate, thalline margin dentate-ciliate, disc up to 1 cm in diameter, imperforate, spores 25–28 × 17–20 μm, thick-walled. Conidia sublageniform, 7–9 μm long.

TLC: the lividic acid complex, atranorin.

The description is based on the Ugandan material. The specimens from West Africa were better developed, with broader lobes and longer cilia.

Parmelia inexpectata is similar to *P. amaniensis* in most important morphological characters, and the two species differ mainly chemically. However, we consider the complexity of the lividic acid group of substances to warrant the acceptance of the chemical content as a species specific character in this case. For further discussion, see under 'Circumscription of the species'.

The species is not known outside Africa. In East Africa it is represented only by the type collection of *P. paradoxa* cited above.

Fig. 14 *Parmelia jacarandicola* Krog & Swinscow, holotype (UPS). Rule = 1 cm.

29. Parmelia jacarandicola Krog & Swinscow **sp. nov.** **Fig. 14**

Thallus corticola, griseus. Lobi 1–2 cm lati, crenati, ciliis 0·5–2 (3) mm longis, superne leviter maculati. Soralia isidiaque nulla. Apothecia submarginalia, stipitata, disco perforato. Spori 15–16 × 8–10 μm. Conidia filiformia, 10–15 μm longa. Acidum gyrophoricum, acidum psoromicum, et atranorinum continens.

Thallus corticolous, loosely attached, pale grey. Lobes 1–2 cm broad, crenate, ciliate, cilia 0·5–2 (3) mm long. Upper side smooth to pitted, rugose and cracked towards the centre of the thallus, faintly maculate. Medulla white. Underside black, with a broad, brown to mottled, naked marginal zone, rhizines fairly coarse, in scattered groups. Soralia and isidia absent. Apothecia submarginal, stipitate, up to 12 mm in diameter, thalline exciple rugose, exciple and stipe strongly maculate, thalline margin smooth, disc perforate, spores 15–16 × 8–10 μm, thin-walled. Conida filiform, 10–15 μm long.

TLC: gyrophoric acid, psoromic acid (+), atranorin.

Type: Kenya. Rift Valley, Nakuru [0° 17′ S, 36° 5′ E], on trunk of *Jacaranda,* 21 March 1968, leg. *Gunnar Gilenstam* no. 2004 (UPS—holotype, O—isotype).

Parmelia jacarandicola may superficially resemble *P. maclayana,* which, however, has sublageniform conidia and different chemical properties. *Parmelia euneta* differs in its larger spores, distinct maculae, and absence of psoromic acid.

The production of psoromic acid is associated with the apothecia. Fertile lobes and the thalline exciple give a PD+ sulphur yellow reaction in the cortex, whereas the medulla reacts PD−. If a sterile lobe is tested with TLC, the presence of psoromic acid may go undetected.

Parmelia jacarandicola may possibly be considered the parent morph of *P. direagens*, a sorediate species in which psoromic acid is associated with the soralia. However, there is a discrepancy in the conidia, which are sublageniform to rodshaped in *P. direagens.* An alectoronic acid producing strain which occurs in *P. direagens* is not yet known in *P. jacarandicola.*

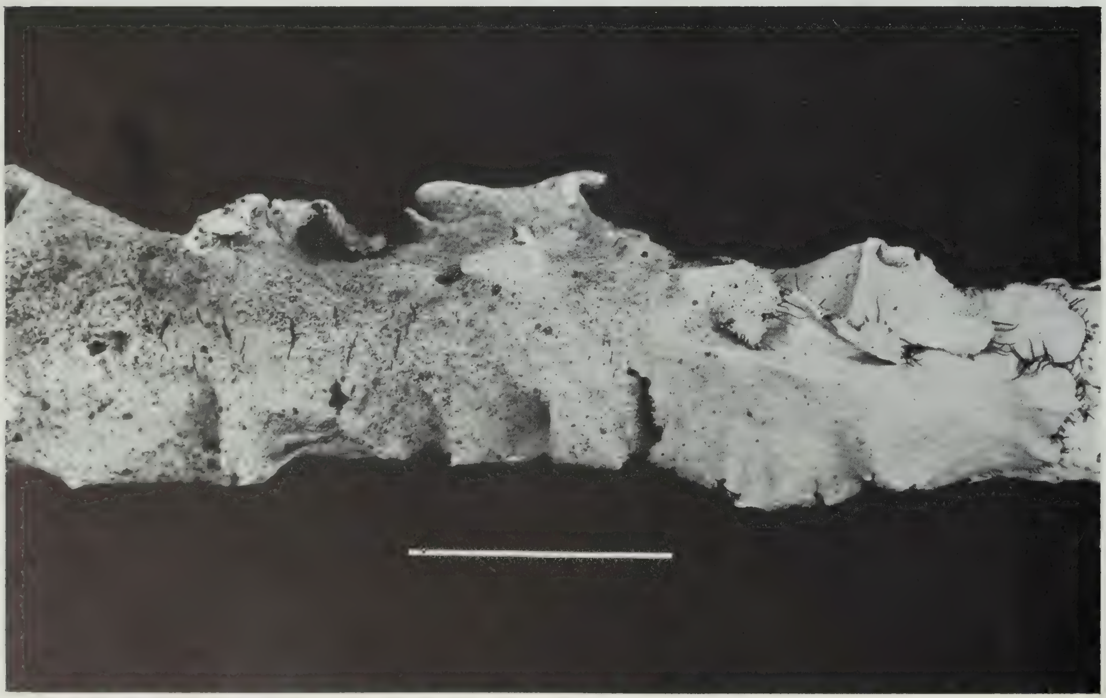

Fig. 15 *Parmelia kwalensis* Krog & Swinscow, holotype (O). Rule = 1 cm.

East African records
Kenya. Rift Valley Province, Nakuru District, Nakuru, Agricultural Show Ground, *c.* 1900 m, on a cultivated *Jacaranda mimosifolia, Santesson* 21663 b (UPS); Nakuru, on trunk of *Jacaranda, Gilenstam* 2004 (UPS, O—type collection).

30. Parmelia kwalensis Krog & Swinscow sp. nov. Fig. 15

Thallus corticola, adnatus, virido-griseus. Lobi ad 1 cm lati, orbiculares, profunde divisi, crenati, ciliis 0·5–2 mm longis, superne maculati. Isidia ad laminam, ad centrum thalli aggregata. Apothecia et pycnidia ignota. Acidum norsticticum, acidum sticticum, acidum consticticum, et atranorinum continens.

Thallus corticolous, adnate, green-grey. Lobes up to 1 cm broad, rounded, deeply divided, crenate, ciliate, cilia 0·5–2 mm long. Upper side distinctly maculate. Medulla white. Underside dark brown, with a narrow, pale brown, naked marginal zone, rhizines relatively long, slender, scattered almost to the margins. Soralia absent. Isidia laminal, crowded towards the centre of the thallus, cylindrical, simple or coralloid, some bearing cilia. Apothecia and pycnidia unknown.

TLC: norstictic acid, stictic acid, constictic acid, atranorin.

Type: Kenya. Coast Province, Kwale District, 2 km N of Gazi, 4° 22′ S, 39° 30′ E, in mangrove, February 1972, coll. *H. Krog & T. D. V. Swinscow* no. K 44/103 (O—holotype, BM—isotype).

Parmelia kwalensis is considered to be the isidiate counterpart of the primary species *P. aldabrensis*, which grows in the same locality.

The species recalls *P. crinita* in being isidiate and ciliate and producing stictic acid, but differs in the strongly maculate upper cortex, brown underside, and presence of norstictic acid. Furthermore, the two species have different ecological requirements, since *P. crinita* is a species of montane forests and inselbergs. *Parmelia subtinctoria*, which has a maculate upper cortex and a brown underside, differs both in chemical properties and ecology; it has not been collected below 1500 m altitude in our area.

Parmelia kwalensis is known only from the type locality where it grew on twigs in a mangrove by the Indian Ocean; we have collected it there on two different occasions.

East African records
Kenya. Coast Province, Kwale District, 2 km N of Gazi, K 44/103 (type collection), 3K 30/136.

31. Parmelia leonis Krog & Swinscow sp. nov. Fig. 16

Thallus corticola, griseus ad griseo-viridis. Lobi 0·5–1 (2) cm lati, orbiculares vel irregulariter incisi,

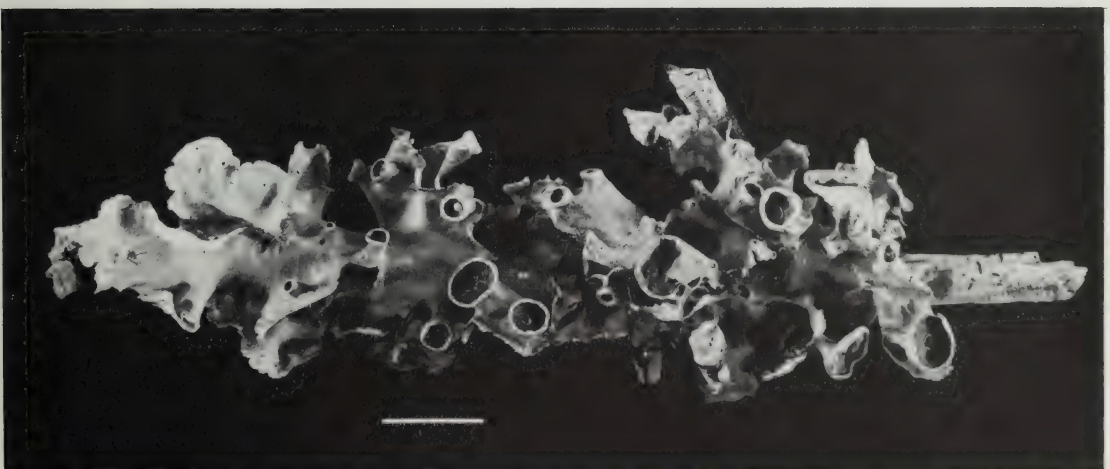

Fig. 16 *Parmelia leonis* Krog & Swinscow, holotype (O). Rule = 1 cm.

crenati, ciliis 0·3–2 mm longis, superne valde maculati, inferne plerumque omnino albi vel raro ad centrum nigri. Soralia isidiaque nulla. Apothecia marginalia vel submarginalia, stipitata, disco vulgo late perforato. Spori 16–18 (20) × 8–10 μm. Conidia filiformia, 12–16 (18) μm longa. Acidum protolichesterinicum et atranorinum continens.

Thallus corticolous, loosely attached, pale grey to grey-green. Lobes 0·5–1 (2) cm broad, rounded or irregularly incised, crenate, ciliate, cilia 0·3–2 mm long. Upper side strongly maculate, cracked and rugose towards the centre. Medulla white. Underside entirely white, or rarely blackened in the centre with a wide white marginal zone, occasionally with brown blotches in unattached parts, strongly rugose, with white, pale brown, black-tipped, or black rhizines. Soralia and isidia absent. Apothecia marginal and submarginal, stipitate, up to 1·5 cm in diameter, thalline exciple rugose, thalline margin entire or rarely dentate-ciliate, sometimes involute, disc mostly widely perforate, spores 16–18 (20) × 8–10 μm. Conidia filiform, 12–16 (18) μm long.

TLC: protolichesterinic acid, atranorin.

Type: Kenya. Eastern Province, Machakos District, lava flow 5 km NW of Kibwezi, 2° 35′ S, 37° 51′ E, on shrubs, 1000 m, February 1974, coll. *H. Krog & T. D. V. Swinscow* no. 3K 23/127 (O—holotype, BM, UPS—isotypes).

Parmelia leonis differs from the protolichesterinic acid strain of *P. abessinica* in the almost entirely white underside and the longly filiform conidia. From *P. glaucocarpoides* Zahlbr. it differs in the same characters, and also in spores size which in *P. glaucocarpoides* is 25–27 × 12–15 μm. *Parmelia melanothrix* (Mont.) Vainio, another primary species with protolichesterinic acid, has imperforate discs and spores 20–26 μm long, fide Hale (1965). *Parmelia leonis* often grows together with *P. uberrima*, which also has a white underside but has imperforate apothecia and contains alectoronic acid, and *P. andina*, which lacks cilia and reacts C+ blood red in the medulla (lecanoric acid).

Parmelia leonis grows on twigs and thinner branches of shrubs in dry, well lit sites. It is locally abundant in the type locality at 1000 m and has further been collected once at 1400 m in Kenya and once at 500–700 m in Tanzania.

East African records

Kenya. Eastern Province, Machakos District, 5 km NW of Kibwezi, 3K 23/127 (type collection), K 20/25B, 120, 2K 22/107, 5K 2/30, Ol Doinyo Sapuk, 20 km SE of Thika, 2K 1/105. **Tanzania.** Eastern Province, Morogoro District, Kitulangalo Forest Reserve, 6 May 1978, *Dahl* (O).

32. Parmelia lobulascens Steiner

Verh. zool.-bot. Ges. Wien **53** : 234 (1903).—*Parmotrema lobulascens* (Steiner) Hale, *Phytologia* **28** : 337 (1974). Type: Cameroons, *Bornmüller* (WU—not seen). [TLC (Hale 1973): alectoronic acid, α-collatolic acid, gyrophoric acid, atranorin.]

Parmelia natalensis Steiner & Zahlbr., *in* Zahlbruckner, *Bot. Jb.* **60** : 515 (1926).—*Parmotrema natalense* (Steiner & Zahlbr.) Hale, *Phytologia* **28** : 337 (1974). Type: Natal, Drakens-Berge, Van Reenens-Pass, Schwarzer Berg, bei 1700 m, *Brunnthaler* (W—not seen).

Parmelia pseudonilgherrensis Asah., *J. Jap. Bot.* **29** : 370 (1954).—*Parmotrema pseudonilgherrense* (Asah.) Hale, *Mycotaxon* **5** : 441 (1977). Type: Korea, Mt Hokusui-Hakusan, Kankyo-Nando, 13 August 1936, coll. *U. Tsutani* (TNS—lectotype). [TLC: alectoronic acid, α-collatolic acid, atranorin.]

Thallus corticolous or saxicolous, often coriaceous, loosely attached, pale grey to grey-green, lobe margins sometimes tinged with brown. Lobes 0·5–1·5 (2) cm broad, rounded and crenate or irregularly incised-dentate, margins ascending or revolute, ciliate, cilia 0·2–3 (5) mm long, coarse or slender, sometimes absent or poorly developed on peripheral lobes but present on lateral and central lobes, rarely entirely lacking. Secondary lobules common along the lobe margins and on the lamina. Upper side distinctly maculate, irregularly cracked, here and there with black, discoloured patches. Medulla white. Underside black, with a brown, naked marginal zone, rhizines fairly long, unevenly

distributed. Soralia linear on ascending lobe margins or submarginal, pustular, and punctiform to confluent on revolute lobes. Apothecia uncommon, submarginal on peripheral or central lobes, usually distinctly stipitate on swollen stipes but sometimes substipitate with a constricted base, thalline exciple strongly rugose, becoming sorediate, thalline margin crenate to lobulate, disc perforate or imperforate, often radially split, spores (13) 20–27 (30) × (8) 10–15 (18) μm, relatively thick-walled. Conidia filiform, (10) 12–16 (18) μm long.

TLC: alectoronic acid, ± α-collatolic acid, ± gyrophoric acid, atranorin.

Hale (1965) found *P. lobulascens* morphologically very close to *P. pseudonilgherrensis*, but at the time the species was believed to contain gyrophoric acid only, while *P. pseudonilgherrensis* had alectoronic and α-collatolic acids. With the application of TLC, Hale (1973) found that *P. lobulascens* had both alectoronic and α-collatolic acids in addition to gyrophoric acid. Winnem (1975) gave the first report of apothecia in *P. lobulascens*, and on the basis of two fertile specimens she found that it had small spores, 13–17 × 8–10 μm. However, as in several secondary species, the apothecia of *P. lobulascens* produced few spores which often gave the impression of being deformed or abnormal (pyriform shape, extremely thin spore wall, shrunken cell content). The same phenomenon was encountered also in specimens of *P. pseudonilgherrensis.* We believe that the non-sorediate counterpart of *P. lobulascens* s. str., classified as *P. diversa* by Hale (1973) and Winnem (1975), gives better information on its normal spore size, namely 20–25 × 10–15 μm, which is within the variation range for *P. pseudonilgherrensis.* Since there is no important morphological, anatomical, or ecological differences between *P. lobulascens* and *P. pseudonilgherrensis*, we regard the gyrophoric acid as an accessory substance and reduce *P. pseudonilgherrensis* to synonymy with *P. lobulascens.*

Parmelia natalensis has been regarded as distinct from *P. lobulascens* (as *P. pseudonilgherrensis*) mainly owing to its submarginal soralia on revolute lobes and its substipitate, imperforate apothecia centrally situated on the thallus, contrasting with the linear soralia on ascending lobe margins and the stipitate, perforate, submarginal apothecia of *P. lobulascens.* Unfortunately, the type of *P. natalensis* has not been available for study, but the exsiccate number 60 in Almborn, Lichenes Africani (LD), collected in Kenya, showed all the diagnostic characters mentioned in the protologue, including rather small spores. The specimen at first sight looked convincingly different from *P. lobulascens*, but when plentiful material was studied, no clear-cut discontinuities could be found. The centrally located apothecia of *P. natalensis* were not equivalent to laminal apothecia; they were merely submarginally situated on central lobes. In *P. lobulascens* the apothecia varied in individual specimens from perforate to entirely imperforate and radially split, while in *P. natalensis* the occasional perforate apothecium occurred in addition to the more common imperforate ones. Most specimens of the *natalensis* morphotype had spores in the interval 20–25 μm, an indication that the smaller spores sometimes seen (and cited, for example, in the protologue) were immature or abnormal. Specimens with abundant submarginal soralia on revolute lobes often had marginal soralia on ascending lobe margins on the same thallus. Some specimens with exclusively submarginal soralia even produced gyrophoric acid as an accessory substance and would have been included in *P. lobulascens* s. str. on chemical criteria.

If we turn to the primary species, no parent morph corresponding to *P. natalensis* has been suggested in the literature, and it would indeed be extremely difficult to keep such a species separate from *P. nilgherrensis.* Within *P. nilgherrensis* it is possible to find specimens with substipitate rather than stipitate apothecia, or with apothecia mainly situated on central lobes, but none of these traits is suitable for the separation of species. We therefore regard *P. natalensis* as conspecific with *P. lobulascens.*

Parmelia lobulascens is a common and widespread species in all four countries of our study, where it grows on both trees and rock throughout the montane forests, extending into the alpine zone; it has been collected between 1800 and 3600 m altitude but is most common

above 2800 m. Outside our area it is known from South and West Africa, Nepal, and Korea (Hale, 1965), as well as from India (BM).

Selected East African records
Ethiopia. See Winnem (1975) under *P. lobulascens*, *P. natalensis*, and *P. pseudonilgherrensis.* **Kenya.** Central Province, Nyeri District, Mt Kenya, W slope, Naro Moru track (numerous coll. between 2200 and 3500 m altitude), Aberdare Mountains, E of Lesatima, K 25/8a. Rift Valley Province, Elgeyo Marakwet District, Cherangani Hills, 10–20 km S of Labot, 2K 7/14a, 2K 8/118, Sogotio Forest 8 km N of Chebiemit, 2K 10/106; Uasin Gishu District, 5 km NW of Timboroa Summit, 2K 19/118; Kericho District, Cheboswa ENE of Kericho 4K 17/117; Nakuru District, 1 km S of Mau Narok, 4K 29/110. Eastern Province, Meru District, Mt Kenya, E side, at Themwe, 3K 16/164, Mt Kenya, N side, Sirimon track, 4K 20/124. **Tanzania.** Northern Province, Masai District, Ngorongoro Crater, *Sipman* 6371A (herb. Sipman); Arusha District, Mt Meru Crater, T 5/126, Arusha National Park, near Ngurdoto gate, T 6/101. **Uganda.** Kigezi District, Bufumbira County, Muhavura, N side, U 16/10. Toro District, Busongora County, 10 km NW of Kilembe, slopes of Ruwenzori, 2U 13/2. Bugisu District, N Bugisu County, 0·5 km NW of ford over Sasa River, 2U 45/9, 18; Manjiya County, near Bukalesi, *Lye* L 13 (herb. Lye).

33. **Parmelia lophogena** des Abb.

Bull. Inst. fr. Afr. noire A, **20** : 19 (1958).—*Parmotrema lophogenum* (des Abb.) Hale, *Phytologia* **28** : 337 (1974). Type: Guinée Française: Fouta-Djalon, à Dalaba, 1200 m, *des Abbayes* (US—isotype). [TLC: gyrophoric acid, fatty acids in the reddenda complex, atranorin.]

Thallus corticolous, membranaceous, loosely attached, pale grey to green-grey. Lobes 0·5–2 cm broad, sparsely crenate or crenate-lobulate, ciliate, cilia 2–4 (5) mm long. Upper side emaculate or faintly maculate, cortex fragile, cracking and flaking, pitted or rugose towards the centre. Medulla white. Underside black, with a wide, brown, naked marginal zone, rhizines sparse, in scattered groups. Coarse isidia and/or granular soredia present along the margins or in a broad marginal zone, laminal cilia not uncommon. Apothecia unknown. Conidia filiform, 12–15 (17) μm long.

TLC: gyrophoric acid, fatty acids in the reddenda complex, atranorin.

We have previously discussed the diversity of the vegetative propagules in *P. lophogena*

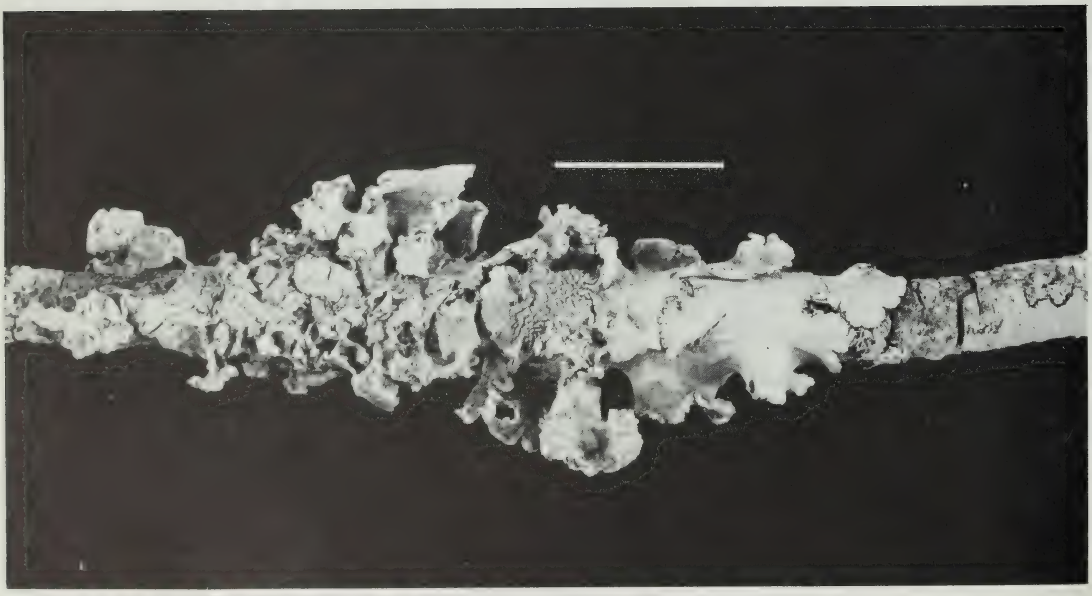

Fig. 17 *Parmelia louisianae* Hale, K 20/119 (○). Rule = 1 cm.

(Krog & Swinscow, 1975), and included *P. diacidula* Hale and *P. dolosa* des Abb. in its variation range.

The species is known only from the African continent and Madagascar (Krog & Swinscow, 1975, Fig. 1). In East Africa it has been collected in Kenya and Tanzania, where it grew in the lower montane forest between 1400 and 2400 m altitude.

East African records

Kenya. Rift Valley Province; Kericho District, Cheboswa ENE of Kericho, 4K 17/115; Laikipia District, Burguret, 4K 25/123; Narok District, Enabilibil, 22 km S of Siape bridge, 4K 31/108. Central Province, Nyeri District, Burguret River, 4K 27/109. Eastern Province, Marsabit District, Mt Marsabit, vicinity of Lake Paradise, 4K 6/138.

For further records from Kenya and Tanzania, see Krog & Swinscow (1975).

34. Parmelia louisianae Hale **Fig. 17**

Phytologia **22** : 92 (1971).—*Parmotrema louisianae* (Hale) Hale, *Phytologia* **28** : 337 (1974). Type: Louisiana, Desoto County, 3 mi N Sabine Co. Line on hwy 175, leg. *M. E. Hale* 34013 (US—holotype). [TLC: alectoronic acid, atranorin.]

Thallus corticolous, loosely attached, pale grey to grey-green. Lobes 0·5–1 cm broad, rounded, margins ascending, crenate, ciliate, cilia 0·5–2 mm long. Upper side maculate, rugose towards the centre. Medulla white. Underside black in the centre, with a broad, white marginal zone, lobe-ends sometimes with brown blotches. Soralia submarginal on revolute lobes. Apothecia not seen. Conidia shortly filiform, 10–12 μm long.

TLC: alectoronic acid, $\pm$ α-collatolic acid, atranorin.

This rare lichen has previously been known from two localities in Louisiana and one in Virginia (W. Culberson, 1973). We have made four small collections of it, all from the same locality in Kenya. Both Hale (1971*b*) and W. Culberson (1973) considered that *P. louisianae* was the sorediate counterpart of the American species *P. rigida* Lynge. Our specimens grew together with *P. uberrima* and might be interpreted as the sorediate counterpart of that species. The two primary species have similar chemical properties except for the addition of norstictic acid in some specimens of *P. rigida*, and they have both got a mainly white underside. However, *P. rigida* differs from *P. uberrima* in having perforate apothecia and longly filiform conidia. The sorediate species has never been found fruiting. No conidia were found in the two American specimens at our disposal, but the Kenyan specimens had the same shortly filiform conidia as *P. uberrima.* As long as *P. louisianae* is known only in a sterile state, its parent morph remains uncertain, and it is not conclusively settled that the American and African populations belong to the same species.

All our specimens grew on shrubs in a thicket in a dry, well lit site at 1000 m altitude.

East African records

Kenya. Eastern Province, Machakos District, lava flow 5 km NW of Kibwezi, K 20/119, 2K 22/109, 3K 23/122, 123.

35. Parmelia maclayana Müll. Arg. **Fig. 18**

Flora, Jena **74** : 376 (1891).—*Parmotrema maclayanum* (Müll. Arg.) Hale, *Phytologia* **28** : 337 (1974). Type: Hb. Maclay, ex Afric. capric. [? collector] (G—holotype, BM—isotype). [TLC: alectoronic acid, unknown with alectoronic acid, atranorin.]

Parmelia procera Steiner & Zahlbr., *in* Zahlbruckner, *Bot. Jb.* **60** : 537 (1926).—*Parmotrema procerum* (Steiner & Zahlbr.) Hale, *Phytologia* **28** : 338 (1974). Type: [Tanzania] E Usambara, near Amani, *Brunnthaler* (US—isolectotype). [TLC: alectoronic acid, α-collatolic acid, atranorin.]

Parmelia breviciliata Hale, *Contr. U.S. natn. Herb.* **36** (5) : 282 (1965).—*Parmotrema breviciliatum* (Hale) Hale, *Phytologia* **28** : 335 (1974). Type: Transvaal, Distr. Pilgrims Rest, 4 miles SE of P. R., on rocks near road, leg. *Ove Almborn* 7800 (LD—holotype). [TLC: alectoronic acid, unknown with alectoronic acid, atranorin.]

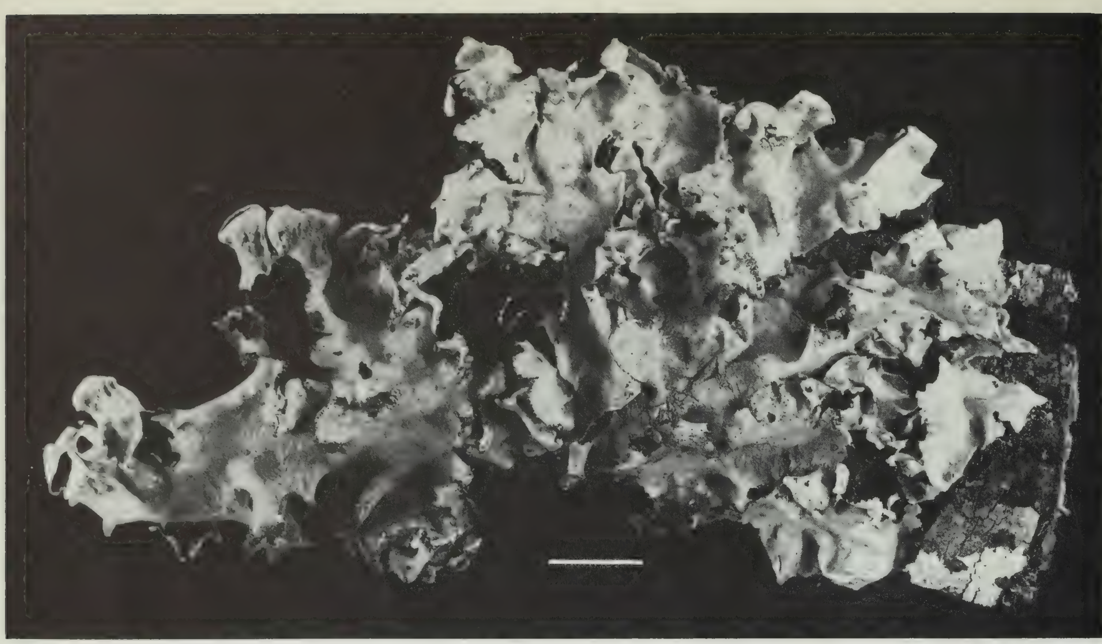

Fig. 18 *Parmelia maclayana* Müll. Arg., *Nordal* INB 849 (O). Rule = 1 cm.

Thallus corticolous or saxicolous, coriaceous, pale grey. Lobes (0·5) 1–2 (2·5) cm broad, entire or crenate-dentate, ciliate, cilia sparse, 0·5–2 (3) mm long. Upper side emaculate, irregularly cracked towards the centre. Medulla white. Underside smooth or rugose, black in the centre, with a dark brown marginal zone, rhizines of medium length, in scattered groups, sometimes coming close to the margins. Soralia and isidia absent. Apothecia submarginal, stipitate, up to 3 cm in diameter, thalline exciple more or less rugose, maculate, thalline margin thin, smooth or weakly crenate, disc imperforate or with a small perforation, spores 12–15 × 7–10 μm. Conidia sublageniform, 6–7 μm long.

TLC: (1) alectoronic acid, unknown with alectoronic acid, atranorin; (2) alectoronic acid, α-collatolic acid, atranorin.

Parmelia maclayana has been separated from *P. procera* mainly by its perforate apothecia. However, this is a variable feature in *P. maclayana*; the only apothecium in one of the type specimens, for example, is imperforate. There is a small chemical difference between them, but it is too slight to warrant the acceptance of two different species. *Parmelia breviciliata* differs from *P. maclayana* only in being saxicolous. The broad lobes, huge apothecia, small, thin-walled spores, and sublageniform conidia are the same in all three taxa. Chemotype (2) is represented only by the type of *P. procera* and by the specimen *Greenway* 1001 cited below; the rest of the specimens belong in chemotype (1).

In East Africa *Parmelia maclayana* has been collected in miombo woodland, artificial habitats, and well lit sites in the lower montane forest between *c.* 900 and 2200 m altitude. We have also seen specimens from Sierra Leone, Cameroon, Zambia, Zimbabwe and Malawi. Hale (1965, under *P. breviciliata*, *P. procera*, and *P. maclayana*) cited numerous collections from continental Africa as well as a few from Madagascar, Thailand, Brazil, and New Caledonia.

East African records

Kenya. Eastern Province, Aberdare Mountains, Kimakia Forest Station, *Ryvarden* 9032 (O). **Tanzania.** E. Usambara, Amani, *Greenway* 1001 (BM); E. Usambara, near Amani, *Brunnthaler* (type of *P. procera*). Lake Province, Bukoba, II/92, *Stuhlmann* 4059 (BM, sub *Parmelia nitens* Müll. Arg.). Southern Province, Songea District, Gumbiro, in miombo woodland, *Nordal* INB 849 (O); Songea

District, Kigonsera, Missionsstation bei Peramiko, *Dietrich* (M). Western Province, Kigoma District, Kungwe-Maheli Peninsula, Kungwe Mountains, September 1959, *Harley* (BM, sub *P. aldabrensis*). **Uganda.** West Mengo District, Busiro County, Entebbe, on epiphytic orchids, *Proctor* s.n. (BM); Naiguru, *Dale* L 49 p. p. (BM).

36. Parmelia mellissii Dodge

Ann. Mo. bot. Gdn **46** : 134 (1959).—*Parmotrema mellissii* (Dodge) Hale, *Phytologia* **28** : 337 (1974). Type: St Helena, coll. *Melliss* 23 (BM—holotype). [TLC (Winnem 1974): alectoronic acid, α-collatolic acid, atranorin.]

Thallus corticolous, membranaceous or rarely somewhat coriaceous, loosely attached, pale grey to grey-green. Lobes 0·3–1 cm broad, margins ascending, crenate, abundantly ciliate, cilia slender, 2–4 mm long. Upper side emaculate, pitted or weakly rugose, cortex fragile, cracking and often flaking, especially near the lobe margins. Medulla white, with patches of an ochraceous, K+ purple pigment (skyrin). Underside black, with a narrow, dark brown marginal zone, rhizines long, slender, in scattered groups. Soralia marginal and submarginal, here and there interspersed with coarse, ciliate isidioid outgrowths which become sorediate with time, soredia granular. Mature apothecia and pycnidia not seen in East African material. (According to Hale (1965) the apothecia are imperforate, with spores 16–22 × 10–14 μm.)

TLC: alectoronic acid, α-collatolic acid, $\pm$ skyrin, atranorin.

Parmelia mellissii recalls *P. cryptoxantha* and *P. lophogena* in its fragile and flaking upper cortex and long cilia. However, *P. cryptoxantha* has mainly laminal pustules and open dactyls with sparse production of soredia, and its medulla is pigmented. *Parmelia lophogena* is a larger, more broad lobed species which differs mainly chemically; it seems to be restricted to Africa.

Parmelia mellissii grows in the lower montane forest, where it has been collected between 2000 and 2400 m altitude. The species is widespread in the Americas and is known from India, the Canary Islands, and St Helena (Hale, 1965), as well as from New Zealand (BM). In East Africa it is rare.

East African records
Kenya. Central Province, Nyeri District, Mt Kenya, above entrance to National Park, 2K 32/4. Eastern Province, Meru District, Mt Kenya, E side, at Themwe, 3K 16/129. **Tanzania.** Northern Province, Arusha District, Mt Meru, confluence of River Jekukumia with River Ngare Nanyuki, T 11/5, 6; Moshi District, Kilimanjaro, Mweka, *Sitari* 280 (TUR).

37. Parmelia nilgherrensis Nyl.

Flora, Jena **52** : 291 (1869).—*Parmotrema nilgherrense* (Nyl.) Hale, *Phytologia* **28** : 338 (1974). Type: Ind. Or., in montib. nilgherrensibus, leg. *Perrottet* (H–NYL 35337—holotype). [TLC: alectoronic acid, α-collatolic acid, atranorin.]

Parmelia diversa Hale, *Phytologia* **27** : 1 (1973).—*Parmotrema diversum* (Hale) Hale, *Phytologia* **28** : 336 (1974). Type: Ethiopia, Bale Prov., mountain pass between Adaba and Goba, 3600 m, January 1972, coll. *H. Krog* E 22/19 (US—holotype, O—isotype). [TLC: alectoronic acid, α-collatolic acid, gyrophoric acid, atranorin.]

Thallus corticolous or saxicolous, usually coriaceous, loosely attached, pale grey, often with a brownish tinge towards the margins. Lobes 1–1·5 (2) cm broad, rounded and crenate or irregularly incised-dentate, margins often ascending, ciliate, cilia 0·2–3 mm long, slender to coarse. Upper side strongly maculate, cracked, sometimes with blackened patches. Medulla white. Underside black, with a brown, naked marginal zone, rhizines slender to coarse, of varying length and density, often penicillate. Soralia and isidia absent. Apothecia up to 2·5 cm in diameter, submarginal, stipitate on often swollen stipes, more rarely substipitate with a constricted base, thalline exciple strongly rugose, thalline margin dentate, involute, disc perforate or imperforate, spores (20) 23–27 (30) × 10–15 μm, fairly thick-walled. Conidia filiform, (10) 12–14 (16) μm long.

TLC: alectoronic acid, ± α-collatolic acid, ± gyrophoric acid, atranorin.

Saxicolous forms at high altitudes are extremely coriaceous, with short, coarse cilia, while corticolous specimens in the montane forests usually have a thinner thallus and longer, more slender cilia. This variation seems to be environmentally induced and is not correlated with the presence or absence of gyrophoric acid. Laminal lobules, which were one of the characteristic features of *P. lobulascens* Steiner, the putative sorediate morph of *P. diversa*, are found in specimens with or without gyrophoric acid. The intermediate spores with a rather thick spore wall as well as the filiform conidia are the same for both chemotypes. We consider gyrophoric acid to be an accessory substance in this case and regard *P. diversa* as conspecific with *P. nilgherrensis*.

Parmelia maclayana differs from *P. nilgherrensis* in its emaculate upper cortex, smaller spores, sublageniform conidia, and different ecological requirements.

Parmelia nilgherrensis is a species of the montane forests, the ericaceous zone, and the low alpine zone; it has been collected between 2000 and 3600 m altitude, but is most common above 2800 m. The gyrophoric acid strain is most widespread in Ethiopia. We have seen only two additional specimens, one from Kenya and one from Tanzania. Outside our area the species is known from Sikkim, India, Sri Lanka, China, and Thailand (Hale, 1965, Fig. 28).

Selected East African records
Ethiopia. Bale Province, Gasore Summit, *Tapper* 960a, 962 (BM). Begemder Province, Semen Nat. Park, Geech plateau, *Heinonen* 1187 (H). Chokke Mts, north of Debra Marcos, C. B. E. E. 34 (BM). For further Ethiopian records, see Winnem (1975) under *P. diversa* and *P. nilgherrensis*. **Kenya.** Central Province, Nyeri District, Mt Kenya, W side, Naro Moru track, K 28/122, 520, Aberdare Mountains, near Karuru-Gura waterfalls, 3K 32/114; Kirinyaga District, Mt Kenya, S side, 2 km NW of Irangi Forest Station, K 48/138. Eastern Province, Meru District, Mt Kenya, E side, at Themwe, 3K 16/167; Rift Valley Province, Elgeyo Marakwet District, Cherangani Hills 10 km S of Labot, 2K 8/190; Trans-Nzoia District, Mt Elgon crater at Maji ya Moto (hot spring), *Hedberg* 912 (UPS). **Tanzania.** Northern Province, Arusha District, Mt Meru Crater, T 5/143. **Uganda.** Bugisu District, N Bugisu County, by Sasa Hut on Mt Elgon, 2U 44/8. Toro District, Busongora County, Mt Ruwenzori, near Nyamileju Hut, *Lye* L 61 (herb. Lye).

38. Parmelia paraphypoptropa W. Culb. **Fig. 19**

Bryologist **76** : 29 (1973).—*Parmotrema paraphypotropum* (W. Culb.) Hale, *Phytologia* **28** : 338

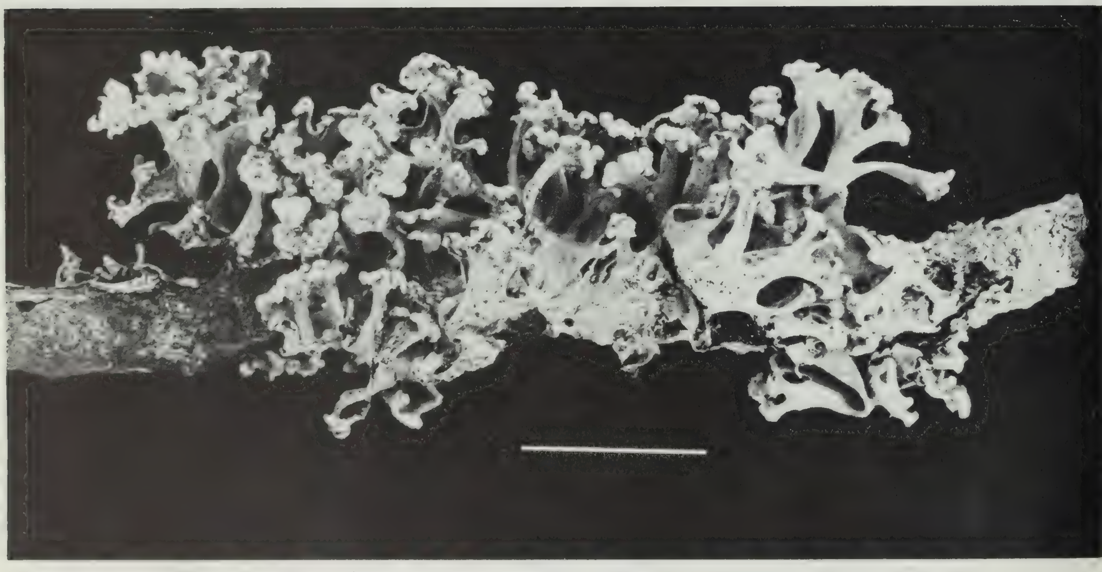

Fig. 19 *Parmelia parahypotropa* W. Culb., 3K 30/107 (○). Rule = 1 cm.

(1974). Type: Formosa, Kural, 250 m, *Kurokawa* 1487 (TNS—holotype). [TLC: norstictic acid, galbinic acid, salazinic acid, atranorin.]

Thallus corticolous, loosely attached, pale green-grey. Lobes up to 0·6 cm broad, deeply divided, laciniae 1·2–1·5 mm broad, sublinear, dichotomously branched, ciliate, cilia 1–2 mm long. Upper side faintly to distinctly maculate, often cracked. Medulla white. Underside black in the centre, with a white or mottled marginal zone mainly restricted to the laciniae, rhizines short, sparse, in the centre of the thallus. Soralia labriform at the tips of the laciniae, soredia farinose. Apothecia and pycnidia not seen.

TLC: norstictic acid, galbinic acid, salazinic acid, ± fatty acid (trace), atranorin.

The narrow laciniae and labriform soralia distinguish *P. parahypotropa* from all other *Amphygmnia* species in our area.

In East Africa *P. parahypotropa* is restricted to the coast of the Indian Ocean, where it has been collected on twigs in mangroves and on the trunk of a *Cocos* at 300 m altitude. It has been reported from similar habitats in Australia by Stevens & Rogers (1979).

East African records

Kenya. Coast Province, Kwale District, Kwale, Forestry Station, *Santesson* 20802b (UPS), 2 km N of Gazi, K 44/34, 110, 3K 30/107; Kilifi District, Mida Creek, 3K 29/115.

39. Parmelia pardii Krog & Swinscow sp. nov. **Fig. 20**

Thallus saxicola, griseus. Lobi 0·8–1·5 (2) cm lati, orbiculares, integri vel leniter crenati, eciliati, superne nitidi, emaculati. Soralia ad lobos laterales, marginalia et linearia, ad laminam punctiformia vel subcapitata, vulgo confluentia. Apothecia laminalia, disco primum imperforato demum perforato. Spori 10–13 × 6–8 μm. Conidia filiformia, 10–14 μm longa. Acidum fumarprotocetraricum, acidum protocetraricum, et atranorinum continens.

Thallus saxicolous, adnate, pale grey. Lobes 0·8–1·5 (2) cm broad, rounded, entire or

Fig. 20 *Parmelia pardii* Krog & Swinscow, holotype (○). Rule = 1 cm.

weakly crenate, eciliate. Upper side shiny, emaculate, more or less cracked and rugose towards the centre. Medulla white. Underside black, with a broad, brown, naked marginal zone, rhizines fairly coarse, mainly black but occasionally brown peripherally, peripheral papillae sometimes present. Soralia marginal and linear on lateral lobes and punctiform to subcapitate on the lamina, often confluent over larger areas, soredia granular. Apothecia laminal, thalline exciple sorediate, disc at first imperforate, becoming perforate with age, spores 10–13 × 6–8 μm. Conidia filiform, 10–14 μm long.

TLC: fumarprotocetraric acid, protocetraric acid, atranorin.

Type: Kenya. Eastern Province, Machakos District, Lukenia, 30 km SE of Nairobi, 1° 28′ S, 37° 04′ E, on rock and over plant remains, 1750 m, February 1974, coll. *H. Krog & T. D. V. Swinscow* no. 3K 1/102 (O—holotype; BM, UPS—isotypes).

Parmelia pardii recalls *P. pseudograyana* in chemical properties and in its saxicolous habit. However, that species has marginal cilia, imperforate apothecia, and sublageniform conidia. Morphologically *P. pardii* is close to *P. defecta*, with which it sometimes grows. The apothecia of *P. defecta* are not known, but in its supposed parent morph *P. soyauxii* they are distinctly perforate. That, and the considerable difference in chemistry, made us decide not to include *P. pardii* in *P. defecta* as a chemical strain. Fumarprotocetraric acid is the main diagnostic compound of *P. pardii*, while the much more commonly occurring protocetraric acid is present in lower concentrations

Parmelia pardii is a species of exposed acidic rock. It has been collected at 1650–1750 m altitude.

East African records
Kenya. Eastern Province, Machakos District, Lukenia, 30 km SE of Nairobi, 3K 1/102 (type collection). Coast Province, Taita District, N of Mwanda summit, 2K 28/107; Taita District, E of Mwanda summit, 2K 29/102.

40. Parmelia perlata (Huds.) Ach.

Meth. Lich. : 216 (1803).—*Lichen perlatus* Huds., *Fl. Angl.* : 448 (1762).—*Parmotrema perlatum* (Huds.) Choisy, *Bull. mens. Soc. linn. Lyon* **21** : 174 (1952). Type: Specimen and pl. 20, fig. 39B, Dillenius, *Hist. Musc.* : 147 (1742 ['1741']) (OXF—lectotypotype, not seen).

Thallus corticolous, membranaceous, loosely attached, pale grey to grey-green. Lobes 0·5–1·2 cm broad, margins ascending, crenate, ciliate, cilia 0·5–1·5 mm long. Upper side emaculate to faintly maculate, pitted and uneven, often cracked. Medulla white. Underside black in the centre, with a brown marginal zone, densely rhizinate, rhizines short, sometimes extending almost to the margins. Soralia marginal, linear to subcapitate on somewhat revolute lobes, sometimes spreading submarginally. Apothecia and conidia not seen in East African material. (According to Hale (1965) the apothecia are imperforate with spores 22–30 × 13–16 μm.)

TLC: stictic acid, constictic acid, atranorin.

Parmelia perlata is closely related to *P. bangii*, a species which differs in having submarginal, pustular soralia and a fragile and flaking upper cortex.

In East Africa we have collected *P. perlata* in inselbergs, montane forests, and the ericaceous zone between 1400 and 3100 m altitude. The species is pantemperate and widespread in both the northern and southern hemispheres (Hale, 1965, Fig. 20).

East African records
Ethiopia. Sidamo Province, between Kebre Mengist and Wadera, *Winnem* 595/5, 6 (O). **Kenya.** Central Province, Nyeri District, Mt Kenya, W side, above entrance to National Park, K 32/110, Mt Kenya, Naro Moru track, upper forest, 3100 m, K 35/105, Aberdare Mts, 10 km W of Tusha, 3K 31/104. Rift Valley Province, Nakuru District, Londiani Forest SE of Mau Summit, 2K 5/106. Eastern Province, Marsabit District, vicinity of Lake Paradise, 4K 6/139. **Tanzania.** Northern Province, Arusha District, Mt Meru, confluence of River Jekukumia with River Ngare Nanyuki, T 11/114, 128.

41. Parmelia permutata Stirton

Scott. Nat. **4** : 252 (1877–78).—*Parmotrema permutatum* (Stirton) Hale, *Phytologia* **28** : 338 (1974). Type: Queensland, Brisbane, *I. M. Bailey* 25 (BM—holotype). [TLC: gyrophoric acid, pigment, atranorin.]

Thallus corticolous, loosely attached, pale grey to grey-green. Lobes 0·5–1·5 cm broad, weakly crenate, ciliate, cilia 1–3 (4) mm long. Upper side emaculate, smooth to faintly pitted, cracked in older parts. Medulla yellow, ochraceous, or salmon pink, pigment K−. Underside black, with a broad, brown or mottled, naked marginal zone, rhizines sparse, in groups. Soralia marginal, linear, often spreading submarginally. Apothecia absent. Pycnidia present but conidia not found.

TLC: gyrophoric acid, pigment, atranorin.

If the medullary pigment is overlooked, *P. permutata* may be confused with *P. sancti-angelii*, another emaculate, sorediate species with gyrophoric acid. However, in *P. permutata* the gyrophoric acid is concentrated near the upper cortex, giving a red reaction upon application of C, while the rest of the medulla remains yellowish pink.

In East Africa *P. permutata* is a species of artificial habitats and well lit sites in the lower montane forest. It has been collected between 1100 and 2400 m altitude in all four countries of our study. Outside Africa it is widespread, being known from Australia (type), India, Sumatra, and Haiti (Hale, 1965), Papua New Guinea (Kurokawa, 1979), and Brazil (W, O).

East African records

Ethiopia. See Winnem (1975). **Kenya.** Eastern Province, Machakos District, Ol Doinyo Sapuk, 20 km SE of Thika, 2K 4/105. Coast Province, Taita District, W of Wundanyi, 2K 25/103. Rift Valley Province, Kericho District, Kericho Tea hotel, 4K 7/106. **Tanzania.** Northern Province, Arusha District, Arusha National Park, Juniper Hill, T 3/120. **Uganda.** East Mengo District, Kyagwe County, Owen Falls Dam, facing Jinja, U 4/15. Toro District, Burahya County, street in Fort Portal, 2U 17/11. Kigezi District, Kinkizi County, 30 miles NW of Kabale, Impenetrable Forest, *Burnet* AMB 213 (BM).

42. Parmelia pigmentifera Krog & Swinscow **sp. nov.** **Fig. 21**

Thallus corticola, griseus. Lobi 0·5–0·8 cm lati, ciliis 0·5–2 (3) mm longis, superne emaculati. Medulla pigmento ochraceo, K−. Soralia isidiaque nulla. Apothecia marginalia vel submarginalia, stipitata, margine thallino laevi ad leniter dentato, ciliato, disco imperforato. Spori 18–22 (24) × 10–12 (14) μm. Conidia leniter sublageniformia, 7–8 μm longa. Acida ignota, pigmentum, et atranorinum continens.

Thallus corticolous, loosely attached, pale grey. Lobes 0·5–0·8 cm broad, ciliate, cilia 0·5–2 (3) mm long. Upper side emaculate, often pruinose, smooth, becoming rugose with age. Medulla pigmented, pigment pink to ochraceous, K−. Underside black, with a brown, naked marginal zone, rhizines sparse. Soralia and isidia absent. Apothecia marginal and submarginal, stipitate, stipe often formed by a convoluted lobe, thalline exciple and stipe strongly maculate, thalline margin smooth to weakly dentate, ciliate, disc up to 1 cm in diameter, imperforate, spores 18–22 (24) × 10–12 (14) μm. Pycnidia numerous, conidia weakly sublageniform, 7–8 μm long.

TLC: two undetermined substances in the following Rf classes. TDA: 2–3, 4; HEF: 4–5, 6; and TA: 2–3, 5–6, giving a strong bluish white fluorescence under long-wave UV light; undetermined pigment, atranorin.

Type: Kenya. Coast Province, Kilifi District, Mida Creek, edge of mangrove, 3° 22′ S, 39° 57′ E, February 1974, coll. *H. Krog & T. D. V. Swinscow* no. 3K 29/112 (O—holotype; BM, UPS—isotypes).

Most primary *Amphigymnia* species with a pigmented medulla differ from *P. pigmentifera*, among other characters, in having larger spores. An exception is *P. subcolorata* (also

Fig. 21 *Parmelia pigmentifera* Krog & Swinscow, holotype (O). Rule = 1 cm.

occurring in East Africa), which, however, has perforate apothecia, filiform conidia, and different ecological requirements.

Parmelia pigmentifera grows on twigs in mangroves on the Kenyan coast, and has also been collected at 70 m altitude near the coast in Tanzania.

East African records

Kenya. Coast Province, Kilifi District, Mida Creek, 3K 29/112 (type collection). **Tanzania.** Eastern Province, Rufiji District, Ngulakula, in miombo woodland, *Nordal* INB 758 (O).

43. Parmelia pilosa Stizenb.

Ber. Tät. St Gall. naturw. Ges. **1888–89** : 165 (1890).—*Parmelina pilosa* (Stizenb.) Hale, *Phytologia* **28** : 483 (1974). Type: Republic Oranje, saxicola in montibus trachyticis Taaibosch-Kranz ad Rhenoster-Rivier, *Rehmann* (ZT—lectotype, not seen).

Thallus corticolous or rarely saxicolous, usually adnate, pale grey to slate grey. Lobes deeply divided, 0·5–1 (1·5) cm broad, crenate, ciliate, cilia coarse, 0·2–1 (2) mm long, often branched. Upper side distinctly maculate, sometimes partly pruinose. Medulla white. Underside black, with a brown marginal zone, usually rhizinate to the margins, rhizines dimorphous, in part long and coarse, in part short and slender. Soralia laminal to submarginal, punctiform. Apothecia not seen in East African material. Conidia filiform, 12–16 μm long.

TLC: undetermined fatty acid, atranorin.

Parmelia consors Nyl., not known from East Africa, is considered to be the parent morph of *P. pilosa* (Hale, 1976*b*). Since it has partly perforate apothecia and filiform conidia we believe that the species pair is better placed in *Amphigymnia* than in genus *Parmelina* Hale (=subgenus *Cyclocheila* (Vainio) Krog & Swinscow). Species with dimorphous rhizines extending to the margins, such as *P. subsumpta*, are already accommodated in *Amphigymnia*.

Parmelia pilosa has been collected on trunks and branches of solitary trees, often in

artificial habitats, rarely on rock, in well lit sites between 1300 and 2000 m altitude. Outside our area it is known from South Africa and South America (Hale, 1976*b*).

East African records
Ethiopia. Shewa Province, Debre Zeit, near Green Lake, *Winnem* 159/12 (O); Wondo Gennet, 20 km S of Shashemenne, E 5/30, *Winnem* 494/12 (O). Sidamo Province, E shore of Lake Awasa, E 6/8, *Winnem* 415/12, 442/10 (O); Awasa, NLM resort, *Winnem* 492/8 (O); Yirga Alem, Sidamo Provincial Hospital, E 20/21; Wadera, *Winnem* 510/18, 512/18, 596/17 (O). **Kenya.** Coast Province, Taita District, vicinity of Wundanyi 2K 25/106, 2K 26/103, 2K 27/137. Rift Valley Province, Samburu District, WSW slope of Warges, 4K 3/115; Kericho District, Kericho Tea Hotel, 4K 16/105. Nyanza Province, Kisii District, 6 km E of Keroka, 4K 11/107, Kisii, 4K 13/104. **Uganda.** Mubende District, Buwekula County, Mubende Hill, 3U 12/3. Masaka District, Buddu County, near Kurumba, *Lye* L 222 B (herb. Lye).

44. **Parmelia planatilobata** Hale

J. Jap. Bot. **40** : 200 (1964).—*Parmotrema planatilobatum* (Hale) Hale, *Phytologia* **28** : 338 (1974). Type: Mountain Garden of Tjibodas, Java, *c.* 1400 m, *Kurokawa* 2160 (TNS—holotype, not seen).

Thallus corticolous or saxicolous, loosely attached, pale grey. Lobes 0·5–0·8 cm broad, rounded, entire or crenate, ciliate, cilia slender, 1–2 mm long. Upper side emaculate. Medulla white, with patches of an ochraceous, K+ purple pigment (skyrin). Underside black, with a brown, naked marginal zone, rhizines long, slender. Soralia absent. Dorsiventral, palmate, ciliate lobules and coralloid, more or less flattened, ciliate isidia abundant near the margins of the lobes, in part also marginally situated. One immature apothecium seen, no spores or conidia.

TLC: gyrophoric acid, ± skyrin, atranorin.

Parmelia planatilobata is apparently rare in East Africa. There are three collections of it, one from rock and two from tree bark. They all grew between 800 and 1000 m altitude in the Usambara Mountains. The species was previously known from Java and Malaya (Hale, 1965).

East African records
Tanzania. Tanga Province, Lushoto District, Usambara Mts, Amani, Dodwe (road towards Derema), *Santesson* 23360 (UPS), Amani, in the surroundings of Forestry House, *Vitikainen* 9308 (H), Amani Forest Reserve, *T. & S. Pócs* 6102/V–C (herb. Pócs).

45. **Parmelia poolii** Dodge **Fig. 22**

Ann. Mo. bot. Gdn **46** : 146 (1959). Based on *Parmelia proboscidea* var. *sorediifera* Müll. Arg., *Flora, Jena* **67** : 615 (1884), non *Parmelia soredifera* Sprengel (1827). Type: Central Madagascar, *Hildebrandt* s.n. (G—lectotype). [TLC: alectoronic acid, unknown with alectoronic acid, atranorin.]

Thallus corticolous or saxicolous, loosely attached, pale grey. Lobes 0·5–2 cm broad, rounded, entire to crenate-dentate, ciliate, cilia sparse to abundant, 0·3–2 (4) mm. Upper side emaculate, shiny, finely cracked over most of the thallus. Medulla white. Underside black, with a dark brown, naked marginal zone, rhizines short to medium, in scattered groups. Soralia mainly lateral, marginal, linear to subcapitate. Apothecia not seen. Conidia sublageniform, 7–8 μm long.

TLC: (1) alectoronic acid, unknown with alectoronic acid, atranorin; (2) alectoronic acid, α-collatolic acid, atranorin.

The type specimen of *P. poolii* was saxicolous and obviously represents the sorediate counterpart of *P. breviciliata* Hale, which we have reduced to synonymy with *P. maclayana* on the basis of spore and conidium characters (see above under *P. maclayana*).

Parmelia poolii was considered conspecific with *P. rampoddensis* Nyl. by Hale (1965). However, type specimens of *P. rampoddensis* (H, S) indicate a fairly small species with

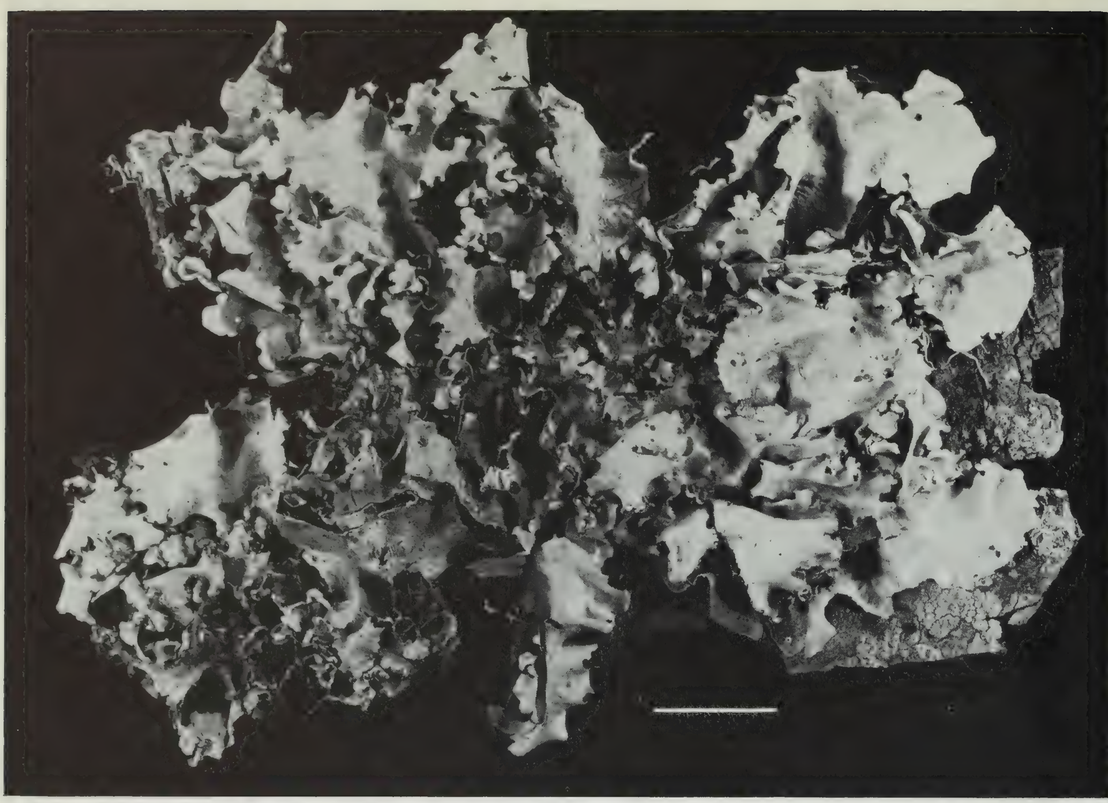

Fig. 22 *Parmelia poolii* Dodge, 2K 6/115 (O). Rule = 1 cm.

marginal soralia on involute lobes, abundant laminal soralia, a pale, mottled marginal zone on the underside, and abundant cilia which produce a purple pigment never seen in East African material. No conidia were found in the type specimens, but a specimen from Sri Lanka, Pidurutalagala, 12 January 1972, *Dahl* (O), corresponding to the type in every respect, produced rod-shaped conidia *c.* 6 μm long. We doubt whether *P. rampoddensis* occurs in East Africa. The specimens cited from Ethiopia by Winnem (1975) are too scrappy for positive identification.

Parmelia arnoldii Du Rietz is another emaculate, ciliate, sorediate *Amphigymnia* species with alectoronic and α-collatolic acids. It differs from our specimens mainly in a more membranaceous thallus, which cannot be considered an important character. However, those of our specimens which produced pycnidia had sublageniform conida 7–8 μm long, while European specimens of *P. arnoldii* produced filiform conidia 10–12 (14) μm long. We therefore include our specimens in *P. poolii. Parmelia arnoldii* does not seem to occur in East Africa.

Parmelia lobulascens differs from *P. poolii* in its strongly maculate upper cortex, longly filiform conidia, and accessory gyrophoric acid.

Parmelia poolii has been collected in the lower montane forest in Kenya between 2000 and 2300 m altitude, and in one locality in Tanzania at 900 m. Outside our area we have seen specimens from Thailand (Kurok. Lich. Rar. Exs. no. 36, O), Madagascar (type collection), and Australia (O). Owing to taxonomic confusion its general distribution is not known, but it seems to agree well with that of *P. maclayana.*

East African records

Kenya. Rift Valley Province, Elgeyo Marakwet District, 7 km N of Chebiemit, 2K 6/115. Central Province, Kirinyaga District, Mt Kenya, S slope, 2 km NW of Irangi Forest Station near River Ena,

K 48/124; Nyeri District, Mt Kenya, S slope, Regati Forest Station, *Ryvarden* 9822b, 9825 (O). Eastern Province, Meru District, Mt Kenya, E slope, on track to Themwe, 3K 15/116. **Tanzania.** Tanga Province, Lushoto District, Usambara Mountains, Amani, in the surroundings of Forestry House, *Santesson* 32153 (UPS).

46. Parmelia praesorediosa Nyl.

Sert. Lich. trop. Labuan Singapore: 18 (1891).—*Parmotrema praesorediosum* (Nyl.) Hale, *Phytologia* **28** : 338 (1974). Type: Singapore, 30 November 1879, *E. Almquist* (H–NYL 35547—holotype, S—isotype). [TLC: fatty acids in the reddenda group, atranorin.]

Parmelia mordenii Hale, *Smithson. Contr. Bot.* **4** : 19 (1971).—*Parmotrema mordenii* (Hale) Hale, *Phytologia* **28** : 337 (1974). Type: Dominica, north of Coulibistri, *c.* 30 m, *Hale* 35649 (BM—isotype). [TLC: fatty acids in the reddenda group, atranorin.]

Thallus corticolous or saxicolous, adnate, pale grey. Lobes 0·4–0·8 (1) cm broad, rounded, entire or crenate, eciliate, sorediate margins ascending. Upper side dull, emaculate, slightly rugose and cracked in older parts. Medulla white. Underside black, with a white, mottled, or brown marginal zone, rhizines short, sparse. Soralia marginal, linear to sublabriform, sometimes spreading on to the lamina and then punctiform to subcapitate. Apothecia not seen in East African material. (According to Hale (1965) the apothecia are imperforate and the spores 15–21 × 7–10μm.) Pycnidia rare, conidia sublageniform, 7–8 μm long.

TLC: fatty acids in the reddenda group, atranorin. (Medulla K+ yellow.)

Hale (1971*a*) distinguished *P. praesorediosa* from *P. mordenii* by its corticolous habit, generally smaller, shorter lobes, thinner, more greenish thallus, finer soredia often produced in linear, crescent-shaped, or labriform soralia without formation of subfatiscent structures, and the K− or faint K+ yellow reaction in the medulla (against K+ yellow in *P. mordenii*). We have found no differences in the medullary reactions between the corticolous and the saxicolous specimens in our area. All other differences are small and can be ascribed to the difference in substrate. The rather small lobes, ascending margins, dull, emaculate upper cortex, chemical properties, and ecological requirements are the same (in one of our localities, a lava flow in Kenya at 1000 m altitude, the species was found both on shrubs and rock, and there was no difference between them). We therefore reduce *P. mordenii* to synonymy with *P. praesorediosa.*

In our area the saxicolous form has been collected in Ethiopia, Kenya, and Uganda, the corticolous form in Kenya and Tanzania, both in fairly dry, well lit sites between *c.* 700 and 1800 m altitude. The species is pantropical to southern temperate, with its main distribution area in Central America (Hale, 1965).

East African records

Ethiopia. Shewa Province, Wondo Gennet, *Winnem* 422/6, 7 (O). Sidamo Province, W of Dilla, E 19/4. **Kenya.** Eastern Province, Machakos District, lava flow 5 km NW of Kibwezi, K 20/104, 105, 504. **Tanzania.** Eastern Province, Morogoro District, Kitulangalo Forest Reserve, 6 May 1978, *Dahl* (O); Morogoro District, *c.* 25 km N of Morogoro, on the way to Dodoma, 3 May 1978, *Dahl* (O); Morogoro District, Morogoro, above university campus, 30 April 1978, *Dahl* (O). **Uganda.** East Mengo District, Kyagwe County, Owen Falls Dam, facing Jinja, U 5/1–2, 10. Masaka District, Bukoto County, rock outcrop by road to Lake Nabugabo, 3U 23/3, 4.

47. Parmelia pseudocrinita des Abb.

Bull. Inst. fr. Afr. noire A, **20** : 19 (1958).—*Parmotrema pseudocrinitum* (des Abb.) Hale, *Phytologia* **28** : 338 (1974). Type: Guinea, Fouta-Djalon Mountains, Dalaba, 5 February 1951, *des Abbayes* (REN—lectotype, not seen).

Thallus corticolous, rarely saxicolous, coriaceous, adnate to loosely attached, pale grey, grey, or grey-green. Lobes 0·5–1 (1·5) cm broad, rounded, crenate, ciliate, cilia 1–2 mm long. Upper side smooth, often shiny, emaculate. Medulla white. Underside black, with a brown,

naked marginal zone, rhizines abundant, long, sometimes branched. Soralia absent. Isidia cylindrical, simple or branched, often ciliate, abundantly produced over most of the thallus. Apothecia rare, laminal, up to 5 mm in diameter, thalline exciple isidiate, disc at first imperforate, becoming perforate, spores 15–18 × 6–8 (10) μm. Conidia filiform, 10–12 μm long.

TLC: gyrophoric acid, atranorin.

Parmelia pseudocrinita has its main distribution area in Africa south of the Sahara. In East Africa we have collected it in fairly well lit sites in inselbergs, riverine and low montane forests, and artificial habitats such as parklands and town avenues. It was mainly found between *c.* 700 and 1800 m altitude, with the exception of one collection from 2600 m. The species is also known from Thailand (Kurokawa, Lich. Rar. Crit. Exs. no. 33 (O)).

East African records

Ethiopia. See Winnem (1975). **Kenya.** Coast Province, Taita District, near school W of Wundanyi, 2K 27/112. Eastern Province, Machakos District, Ol Doinyo Sapuk, 20 km SE of Thika, 2K 4/106; Meru District, near Chogoria, 3K 7/112. Western Province, Kakamega District, Kakamega Forest by River Ikuyawa, 4K 10/108. **Tanzania.** Northern Province, Arusha District, Mt Meru Crater, T 5/154, Arusha National Park, near Ngurdoto Gate, T 6/103. Eastern Province, Morogoro District, Kitulangalo Forest Reserve, 6 May 1978, *Dahl* (O). Tanga Province, Lushoto District, Usambara Mts, Amani, Dodwe (road towards Derema), *Vitikainen* 9412, 9413 (H). **Uganda.** West Mengo District, Busiro County, 3 km SW of Funjo Church, U 2/2, 5, 10; Kyadondo County, Makerere University grounds, U 1/2. Ankole District, Igara County, Kalinzu Forest, 2U 16/29–1.

48. Parmelia pseudograyana Hale

Phytologia **27** : 2 (1973). Type: South Africa, Natal, Drakensberg, Cathedral Peak area, Nhlonhlo Valley, 1500 m, *E. A. Schelpe* 1021 (BOL—holotype, not seen).

Thallus saxicolous, firmly attached, pale grey to ash grey. Lobes 0·5–1 cm broad, with ascending margins, deeply crenate, ciliate, cilia 0·2–1 (2) mm long. Upper side emaculate, usually shiny, matt and rugose towards the centre. Medulla white. Underside black, with a dark brown, naked marginal zone, rhizines fairly coarse, scattered, black to brown. Soralia on lateral lobes, marginal and linear to submarginal and punctiform, soredia often dark grey. Only immature apothecia seen. Conidia rod-shaped to weakly sublageniform, 8–9 μm long.

TLC: fumarprotocetraric acid, protocetraric acid, atranorin.

Parmelia pseudograyana is very close to *P. grayana*, and, as Hale (1973) pointed out, the two species are morphologically indistinguishable. The conidia are also the same. Since mature apothecia have not yet been found in *P. pseudograyana*, we have been unable to compare spore size, but most saxicolous Amphigymnias in our area have small spores. If we hesitate to reduce *P. pseudograyana* to synonymy with *P. grayana* it is because their diagnostic medullary substances are not closely related; furthermore, *P. pseudograyana*, although more common in East Africa, has a much more restricted distribution than *P. grayana*.

Parmelia taitae, newly described in this work, may be regarded as the parent morph of *P. pseudograyana*.

Parmelia pseudograyana grows on acidic rock in dry, well lit sites and in our area has been collected between 1400 and 1900 m altitude. It also occurs in South and West Africa, but is not yet known outside the African continent.

East African records

Ethiopia. Sidamo Province, between Shashemenne and Malge Wondo, *Winnem* 489/2 (O). **Kenya.** Rift Valley Province, Nakuru District, entrance of Masai Gorge N of Lake Naivasha, K 30/108. Eastern Province, Machakos District, Lukenia, 30 km SE of Nairobi, 3K 1/134. Coast Province, Taita District, vicinity of Mwanda Summit, 2K 28/106, 2K 29/101, 2K 31/103. **Tanzania.** [? Southern Province, Songea District] Lupembe, Ludeka, Eusebia (F, fide Hale (1973), not seen). **Uganda.** Kigezi District,

Rubanda County, 1 km W of Hamurwa, 3U 46/3. Ankole District, Igara County, 1 km E of Lubare Ride Pass, *Lye* L 398 (herb. Lye).

49. Parmelia rava Krog & Swinscow sp. nov. — Fig. 23

Thallus corticola, ravus. Lobi 0·5–1 (1·5) cm lati, integri vel leniter crenati, eciliati, superne emaculati. Soralia marginalia, vulgo ad laminam extensa, sorediis granulosis. Apothecia ad laminam, disco imperforato. Spori 18–20 (22) × 8–10 μm. Conidia filiformia, 10–12 μm longa. Acidum protocetraricum, acidum usnicum, et atranorinum continens.

Thallus corticolous, adnate or loosely attached, pale yellow-grey. Lobes 0·5–1 (1·5) cm broad, entire or weakly crenate, eciliate. Upper side emaculate, matt, more or less rugose and cracked towards the centre. Medulla white. Underside black, with a brown, naked marginal zone, rhizines short. Soralia marginal and linear on peripheral lobes, subcapitate on ascending lateral lobes, often spreading laminally, soredia granular, pale green-grey. Apothecia sparse, laminal, thalline exciple sorediate, disc imperforate, spores 18–20 (22) × 8–10 μm. Pycnidia rare, conidia filiform, 10–12 μm long.

TLC: Protocetraric acid, ± fatty acid, usnic acid, atranorin.

Type: Ethiopia. Sidamo Province, 5 km NW of Zenbe Woha, open woodland, 1770 m, 10 January 1972, coll. *H. Krog* no. E 12/5 (O—holotype, BM, UPS—isotypes).

Winnem (1975) determined specimens of *P. rava* from Ethiopia as *P. dominicana* Vainio, another sorediate *Amphigymnia* species with protocetraric acid, usnic acid, and atranorin. However, she noted that the soralia of the Ethiopian specimens were not distinctly yellow in contrast to those of the type specimen. *Parmelia dominicana* can be distinguished from *P. rava* by its mainly grey upper cortex, yellow soralia, slightly smaller spores, and sub-lageniform conidia *c.* 6 μm long. It has not been correctly reported from Africa.

Parmelia rava cannot be distinguished from *P. dilatata* in the sterile state without a

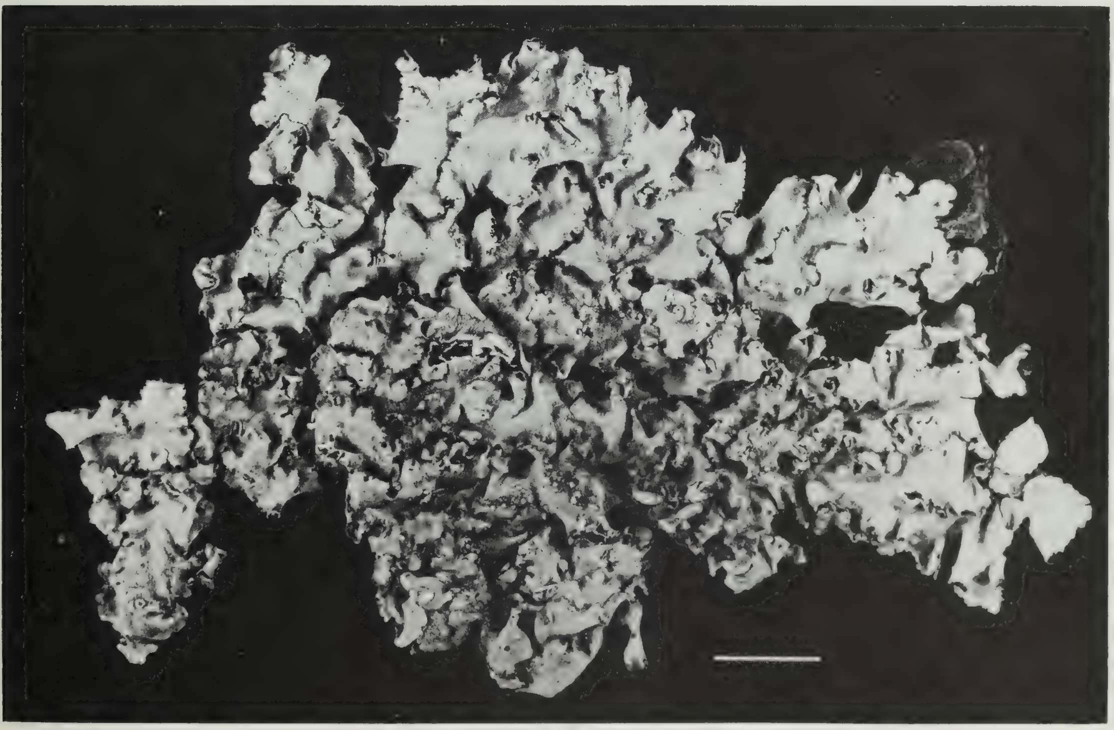

Fig. 23 *Parmelia rava* Krog & Swinscow, holotype (O). Rule = 1 cm.

chemical test, but aside from a more complex chemistry, *P. dilatata* has larger spores, 25–27 μm long.

Parmelia rava is present in all four countries of our study. It has been collected on trees and shrubs in bushed grassland and open woodland betwen 1250 and 1800 m altitude. Outside our area we have seen specimens from south-west and south-east Africa.

East African records
Ethiopia. Sidamo Province, W of Dilla, *Winnem* 470/15 (O); 6 km NW of Wadera, E 10/6; 5 km NW of Zenbe Woha, E 12/5 (type collection). **Kenya.** Eastern Province, Machakos District, lava flow 5 km NW of Kibwezi, 3K 23/128. **Tanzania.** Southern Highlands Province, Iringa District, 50 km S of Iringa along road to Mbeya, *Bjørnstad* AB 1389–h (O); Iringa District, Ruaha National Park, in *Brachystegia* woodland at Magangwe Airstrip, *Bjørnstad* AB 1499–d (O). **Uganda.** Masaka District, Mawogola County, 5 km NW of Ntusi, *Lye* L596 (herb. Lye).

Additional specimens studied
Angola. Bié, between Coemba and Munhango, 1300–1400 m, 10 February 1960, *Degelius* (herb. Degel.). Malanje, Duque de Braganca, 1100 m, 6 March 1960, *Degelius* (herb. Degel.). Moxico, Vila Lus., Rio Dala, 1300 m, 13 February 1960, *Degelius* (herb. Degel.); between Luso and Cachipoque, 1300 m, 16 February 1960, *Degelius* (herb. Degel.); Lucusse, River Lunqué-Bungo, 1200 m, 13 February 1960, *Degelius* (herb. Degel.). **Zaïre.** Southwest of Albertville [Kalemi], 5 March 1930, *Høeg* (TRH). **Zambia.** Mt Makulu Research Station near Chilanga, *Angus* M 1692 (BM). **Zimbabwe.** South of Felixburg, 4 February 1930, *Høeg* (TRH). Mazse District, Christon Bank, *Letcher* 17 (BM). **Moçambique.** Nyassa, Mt Massangulo, *Sousa* 12 (BM). **Malawi.** Ncheese Forest Reserve, *Burtt Davy* 1418 (BM).

50. Parmelia reticulata Taylor

in Mackay, *Flora Hibernica* **2** : 148 (1836).—*Parmotrema reticulatum* (Taylor) Choisy, *Bull. mens. Soc. linn. Lyon* **21** : 175 (1952). Type: Ireland, Kerry County, near Dunkerron (not seen).

Parmelia pseudoreticulata Tavares, *Port. Acta biol.* **1** B : 138 (1945).—*Parmotrema pseudoreticulatum* (Tavares) Hale, *Phytologia* **28** : 338 (1974). Type: Portugal, Estremadura, Arredores de Lisboa (LISU—holotype, not seen).

Parmelia simulans Hale, *Phytologia* **22** : 32 (1971).—*Parmotrema simulans* (Hale) Hale, *Phytologia* **28** : 339 (1974). Based on *Parmelia macrocarpoides* var. *subcomparata* Vainio, *Acta Soc. Fauna Flora fenn.* 7 (7) : 43 (1890). Type: *Vainio*, Lichenes Brasilienses Exs. 918, Minas Geraës, Sitio, 1885 (BM—isolectotype). [TLC: caperatic acid, atranorin.]

Thallus corticolous, saxicolous, or terricolous, membranaceous to coriaceous, loosely attached, pale grey, ash grey, or grey-green. Lobes 0·5–1·5 (2) cm broad, in part rounded and deeply crenate, in part irregularly incised and laciniate, sparingly to moderately ciliate, cilia 0·2–2 mm long. Upper cortex reticulately maculate and cracked. Medulla white. Underside black, rhizinate or papillate to the margins or with a brown, naked marginal zone, rhizines abundant, simple or squarrose. Soralia marginal, linear to subcapitate, more rarely submarginal and punctiform to more or less pustular. Apothecia submarginal to laminal, substipitate, thalline exciple sorediate, disc imperforate or narrowly perforate, spores 13–18 × 8–10 μm. Conidia filiform, (8) 12–16μm long.

TLC: (1) salazinic acid, atranorin; (2) caperatic acid; atranorin.

Parmelia reticulata is a species with a wide ecological amplitude and a correspondingly wide morphological variation. Specimens growing in rather dry sites exposed to high light intensity tend to become coriaceous, have weakly developed maculae, and often submarginal soralia, while specimens in moist, shady habitats usually are membranaceous, have marginal soralia, and well developed maculae. A naked marginal zone on the underside may be broad, narrow, or absent. Development of the soralia, whether linear, subcapitate, or pustular, is not correlated with other characters and does not form a basis for a division at species level. We consider that *P. pseudoreticulata* Tavares falls well within the variation range of *P. reticulata*.

Only one of the specimens from East Africa, *Lye* L 31, corresponded to the *simulans* chemotype. However, neither that specimen nor others, from Brazil (BM), showed morphological characters by which to separate *P. simulans* from *P. reticulata*. We strongly suspect that the species pair *P. cetrata*—*P. reticulata* comprises chemotypes with caperatic acid (*P. macrocarpoides* Vainio—*P. simulans*) and norlobaridone (*P. homotoma* Nyl.—*P. commensurata* Hale), as well as salazinic acid, but since most of these chemotypes are absent from our area, we have not studied the problem in detail.

Parmelia reticulata is extremely common and widespread in all countries of our study; it has probably been undercollected in Uganda. Most of the specimens grew between 1500 and 3000 m altitude, but there are also some from around 1000 m and one collection from sea level. Outside our area the species is common and widespread throughout the tropical and temperate regions. The chemical diversity seems to be centred in Brazil.

Selected East African records
Ethiopia. Shewa Province, Wondo Gennet, 20 km S of Shashemenne, E 5/20. Sidamo Province, Wadera, E 8/3, 12 km S of Kebre Mengist, E 13/5, 30 km SE of Hagere Selam, E 15/30, W of Dilla, E 19/6, Yirga Alem, Sidamo Provincial Hospital, *Winnem* 476/22 (O). Gemu Gofa Province, Gidole, E 26/6. Arussi Province, W slope of Mt Chilalo, *Winnem* 751/34 (O). **Kenya.** Central Province, Nyeri District, Mt Kenya, W side, Naro Moru track, K 13/107; Kiambu district, escarpment E of Rift Valley, 35 km NW of Nairobi, K 15/107; Kirinyaga District, Mt Kenya, S side, 2 km NW of Irangi Forest Station, K 48/112. Eastern Province, Machakos District, Mua Hills, 3K 2/121; Embu District, Embu, Izaak Walton Inn, K 53/122; Meru District, Mt Kenya, E side, at Themwe, 3K 16/241, Mt Kenya, N side, Sirimon track, 4K 24/122; Marsabit District, Mt Marsabit, vicinity of Lake Paradise, 4K 6/144. Coast Province, Kwale District, 2 km N of Gazi, in mangrove, K 44/107; Taita District, W of Wundanyi, 2K 26/106. Rift Valley Province, Kajiado District, Ngong Hills, K 45/4; Elgeyo Marakwet District, Cherangani Hills 10 km S of Labot, 2K 8/122; Uasin Gishu District, 5 km NW of Timboroa summit, 2K 19/106; Samburu District, WSW slope of Warges, 4K 3/118; Kericho District, Kericho Tea Hotel, 4K 7/108. Western Province, Kakamega District, Kakamega Forest, 0·5 km SW of Forest Station, 4K 9/116; Nyanza Province, Kisii District, 6 km E of Keroka, 4K 11/108. **Tanzania.** Northern Province, Arusha District, Arusha National Park, Kusare Forest, T 2/123. Morogoro Province, Morogoro District, Uluguru Mts, Morningside Research Station, *Ryvarden* 11572 (O). Tanga Province, Lushoto District, Usambara Mts, Magamba *c.* 4 km N of Lushoto, *Ryvarden* 10910 (O). Southern Province, Mbeya District, between Kimondo and Kikondo, 9 May 1978, *Dahl* (O). **Uganda.** Karamoja District, Matheniko County, southern slopes of Mt Moroto, 2U 35/10. Masaka District, Bukoto County, by Lake Nabugabo, 3U 20/7. Kigezi District, Bufumbira County, 1km NW of Rushasha, at edge of Impenetrable Forest, *Lye* L 31 (herb. Lye).

51. **Parmelia rimulosa** Dodge

Ann. Mo. bot. Gdn **46** : 133 (1959).—*Parmotrema rimulosum* (Dodge) Hale, *Phytologia* **28** : 338 (1974). Type: [South Africa] Table Mountain, *John Macgillivray* s.n. (BM—holotype). [TLC: alectoronic acid, α-collatolic acid, skyrin, atranorin.]

Thallus corticolous, membranaceous, loosely attached, pale grey to grey-green. Lobes 0·5–1·5 cm broad, rounded, entire or weakly crenate, ciliate, cilia slender, 1–3 mm long, mainly on lateral lobes. Upper side emaculate, cortex fragile, cracking and flaking. Medulla white, except for scattered patches of an ochraceous, K+ purple pigment (skyrin), turning dark grey where the cortex has sloughed off. Underside black, with a pale brown, naked marginal zone, rhizines long, slender, unevenly distributed. Soralia laminal, mainly submarginal, pustular, producing granular soredia and corticate granules. Apothecia not seen. (According to Hale (1965) the apothecia are perforate, with spores 20–22 × 10–13 μm.) Conidia shortly filiform, 8–10 μm long.

TLC: alectoronic acid, α-collatolic acid, $\pm$ skyrin, atranorin.

Parmelia rimulosa is a species of inselbergs and montane forests, where it has been collected between 1800 and 2900 m altitude. Outside our area it is known only from South Africa (Hale, 1965).

East African records

Kenya. Rift Valley Province, Kajiado District, Ngong Hills, K 45/111; Elgeyo Marakwet District, Sogotio Forest 8 km N of Chebiemit, 2K 10/107; Uasin Gishu District, 5 km NW of Timboroa Summit, 2K 19/119; Laikipia District, Burguret, 4K 25/125. Central Province, Nyeri District, Mt Kenya, W side, 2K 33/109, Aberdare Mountains, 10 km W of Tusha, 3K 31/140. Eastern Province, Meru district, Mt Kenya, E side, at Themwe, 3K 16/128. **Tanzania.** Northern Province, Arusha District, Mt Meru Crater, T 5/104; Arusha District, Mt Meru, confluence of River Jekukumia with River Ngare Nanyuki, T 11/119.

52. **Parmelia sancti-angelii** Lynge

Ark. Bot. **13** (13) : 35 (1914).—*Parmotrema sancti-angelii* (Lynge) Hale, *Phytologia* **28** : 339 (1974). Type: Brasiliae civit. Rio Grande do Sul, Santo Angelo pr. Cachoeira, 25 January 1893, leg. *G. A. Malme* (S—lectotype). [TLC: gyrophoric acid, atranorin.]

Thallus corticolous or rarely saxicolous, membranaceous to coriaceous, adnate to loosely attached, pale green, grey-green, or pale grey. Lobes 0·5–1·5 cm broad, rounded, crenate, often deeply divided and with ascending lobe margins, cilia slender, 1–3 (4) mm long, simple or bifurcate. Upper side emaculate, more or less folded or rugose towards the centre. Medulla white. Underside black, with a brown or mottled, naked marginal zone, rhizines fairly long, abundant. Soralia marginal, linear, sometimes spreading submarginally, soredia farinose. Apothecia not seen in East African material. (According to Hale (1965) the apothecia have imperforate discs and spores 13–18 × 7–10 μm.) Pycnidia rare, conidia weakly sublageniform, 6–8 (10) μm long.

TLC: gyrophoric acid, atranorin.

In East Africa *P. sancti-angelii* is usually membranaceous and of a distinctly green colour; only rarely does it become more coriaceous and grey-green to pale grey. Some of our specimens come morphologically very close to the type.

Parmelia lophogena is another sorediate species in our area with a membranaceous thallus and gyrophoric acid in the medulla. It differs from *P. sancti-angelii* in having granular soredia often interspersed with isidia, filiform conidia, and fatty acids in addition to the gyrophoric acid. *Parmelia indoafra*, which has farinose soredia and gyrophoric acid, differs in a more coriaceous thallus, filiform conidia, and the presence of norlobaridone. *Parmelia permutata* differs mainly in its pigmented medulla, and *P. subschimperi* in its maculate upper cortex and filiform conidia.

Parmelia sancti-angelii is, in our area, a species of the lower montane forest and of artificial habitats such as parklands, plantations, and town avenues, where it has been collected between 1000 and 2800 m altitude. According to Hale (1965) it is a common and widespread pantropical species.

Selected East African records

Ethiopia. See Winnem (1975). **Kenya.** Central Province, Kirinyaga District, Mt Kenya, S side, 2 km NW of Irangi Forest Station near River Ena, K 48/114; Nyeri District, Mt Kenya Safari Club, 4K 19/114; Fort Hall District, Aberdare Mountains, Kimakia Forest Station *Ryvarden* 9028 (O). Rift Valley Province, Uasin Gishu District, Sclater's Road 10 km SE of Lessos, 2K 18/101. Eastern Province, Meru District, near Chogoria, 3K 7/119. Western Province, Kakamega District, Kakamega Forest by River Ikuyawa, 4K 10/110. **Tanzania.** Northern Province, Arusha District, Arusha National Park, Juniper Hill, T 3/105, Mt Meru, E side, T 10/101; Moshi District, Kilimanjaro, E of Lemosho Glades, *Santesson* 21058 (UPS). Eastern Province, Morogoro District, above Morningside in the Uluguru Mountains, 6 May 1978, *Dahl* (O). **Uganda.** W Mengo District, Busiro County, Entebbe Botanical Garden, U 3/1; Kyadondo County, Makerere Hill, *Burnet* 232 (BM). Toro District, Burahya County, Fort Portal, 2U 17/9. Masaka District, Bukoto County, by Lake Nabugabo, 3U 20/12.

53. **Parmelia soyauxii** Müll. Arg.

Linnaea **9** : 32 (1880).—*Parmotrema soyauxii* (Müll. Arg.) Hale, *Phytologia* **28** : 339 (1974). Type: Pungo Andongo in Angola, 1880, *Soyaux* 246 (G—holotype). [TLC: lecanoric acid, atranorin.]

Thallus saxicolous, coriaceous, adnate, strongly attached, pale grey. Lobes rounded, 0·5–0·8 (1) cm broad, eciliate, more or less imbricate. Upper side emaculate, shiny, matt and somewhat rugose towards the centre, sometimes with secondary lobules. Medulla white. Underside black, with a brown or mottled, naked marginal zone, rhizines short, coarse, sparse. Soralia and isidia absent. Apothecia common, submarginal, stipitate, up to 1 cm broad with age, thalline margin involute, disc perforate, spores 10–13 × 5–8 μm. Conidia filiform, 12–16 (18) μm long.

TLC: lecanoric acid, atranorin.

Parmelia soyauxii may be considered the parent morph of *P. defecta* with which it sometimes grows. In East Africa it has been collected on acidic rock fully exposed to the sun, between 1000 and 2100 m altitude. It is also known from West and South Africa and Madagascar (Hale, 1965).

East African records

Kenya. Rift Valley Province, Uasin Gishu District, rock outcrop near Sergoi, 27 km S of Chebiemit, 2K 9/103. Eastern Province, Machakos District, Lukenia, 30 km SE of Nairobi, 3K 1/118, lava flow 5 km NW of Kibwezi, K 20/24. Coast Province, Taita District, N of Mwanda Summit, 2K 28/104. **Tanzania.** Lake Province, Bukoba District, Bukoba, gegen Uganda, *Stuhlmann* 405 g (G—holotype of *P. nitens* Müll. Arg.). **Uganda.** Kigezi District, Rubanda County, 1 km W of Hamurwa, 3U 46/202. Bunyoro District, Bugangaizi County, 18 km NE of Kakumiro, 3U 67/5. Masaka District, near Towa Forest, Sese, *Thomas* Th 3028 (BM).

54. Parmelia stuhlmannii Dodge

Ann. Mo. bot. Gdn **46** : 137 (1959). Based on *Parmelia nitens* f. *isidiosa* Müll. Arg., *Bot. Jb.* **20** : 255 (1894). Type: [? Tanzania, Seengebiet] Ririre Karapo, *Stuhlmann* 3301 (G—holotype). [TLC: lecanoric acid, atranorin.]

Thallus saxicolous, adnate, strongly attached, pale grey. Lobes 0·6–0·8 cm broad, rounded, entire or crenate, eciliate, more or less imbricate in central parts. Upper side emaculate, shiny. Medulla white. Underside black, with a brown or mottled, often matt marginal zone, rhizines fairly coarse. Isidia laminal, coarse. Apothecia submarginal, substipitate, thalline exciple smooth or isidiate, disc usually perforate at an early stage, spores 11–13 × 6–7 μm. Conidia filiform, 12–16 (18) μm long.

TLC: lecanoric acid, atranorin.

Parmelia stuhlmannii resembles *P. tinctorum* in most important characters, such as small spores, filiform conidia, and the content of lecanoric acid; furthermore, coarse isidia are present in the *pseudotinctorum* morphotype of *P. tinctorum* as here interpreted. However, *P. stuhlmannii* differs in its smaller lobes, strongly attached thallus, and apothecial perforations which are present even in young apothecia; it is always saxicolous, and does not show the variation in vegatative propagules as found in *P. tinctorum.* It is obviously closely related to the primary species *P. soyauxii.* Unfortunately, the type of *P. stuhlmannii* is small and scrappy, and it cannot be entirely ruled out that it might represent *P. tinctorum.* However, in our interpretation of the species we rely on the original description in which it was considered to be a form of *P. nitens* Müll. Arg. (=*P. soyauxii*).

The main character which distinguishes this species from *P. tinctorum* in the field is its strongly attached thallus which makes it difficult to collect without a piece of the rock on which it is growing. An attempt at scraping it off the substrate with a knife usually results in a total fragmentation of the thallus. Saxicolous specimens of *P. tinctorum*, on the other hand, are always easily collected. In fertile specimens of *P. stuhlmannii* the presence of perforations, even in young, cupuliform apothecia, is an added character.

Parmelia stuhlmannii has been collected on acidic rock in dry, well lit sites between 1500 and 2100 m altitude. It is not known outside Africa.

East African records

Kenya. Rift Valley Province, Uasin Gishu District, near Sergoi, 27 km S of Chebiemit, 2K 9/9; Nakuru District, 5 km WNW of Gilgil, 5K 18/8. Coast Province, Taita District, N of Mwanda Summit, 2K 28/104a. [? **Tanzania**] Ririre Karapo, *Stuhlmann* 3301 (G—type collection). **Uganda.** Ankole District, Nyabushozi County, 20 km E of Mbarara, near county boundary, 2U 22/12.

55. **Parmelia subarnoldii** des Abb. **Fig. 24**

Mém. Inst. scient. Madagascar B, **10** : 113 (1961).—*Parmotrema subarnoldii* (des Abb.) Hale, *Phytologia* **28** : 339 (1974). Type: Madagascar, Centrum medium, in silva dicta Manjakatompo, in montibus Ankaratra, ad truncum, 2000 m, 30 July 1956, leg. *des Abbayes* (US—isolectotype). [TLC: protocetraric acid, protolichesterinic acid, atranorin.]

Parmelia deflectens Kurok., *in* S. Kurokawa (Ed.), *Studies on Cryptogams of Papua New Guinea:* 130 (1979). Type: Papua New Guinea, Morobe District, Bulolo, 780 m, *S. Kurokawa* 5810 (TNS—holotype). [TLC: protocetraric acid, alectoronic acid, atranorin.]

Thallus corticolous, membranaceous to coriaceous, loosely attached, pale grey to grey-green, here and there black discoloured. Lobes 0·5–1 (2) cm broad, rounded or irregularly incised, entire or crenate, ciliate, cilia sparse to abundant, slender, 2–4 (6) mm long. Upper side shiny, emaculate or faintly maculate, often uneven and pitted. Medulla white, with occasional patches of an ochraceous, K+ purple pigment (skyrin). Underside black, with a

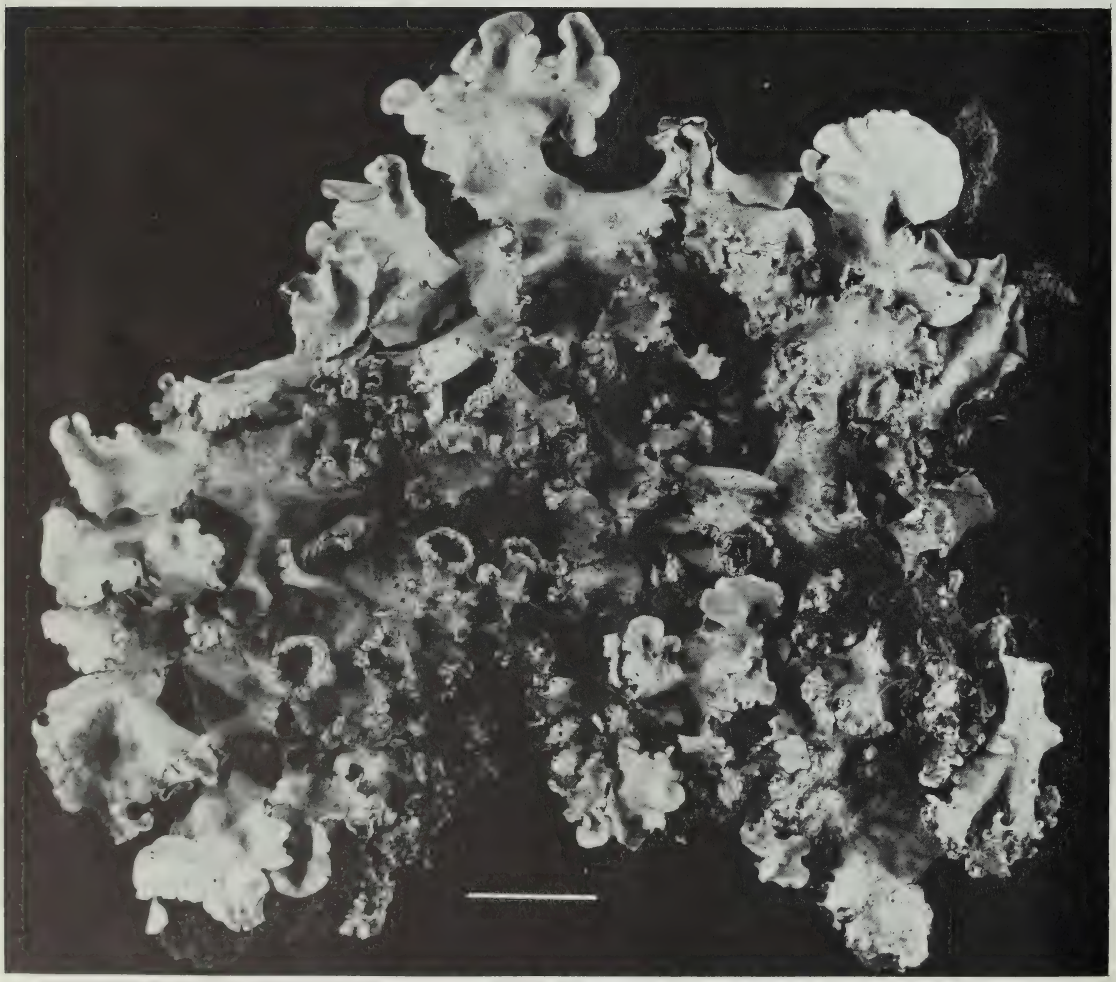

Fig. 24 *Parmelia subarnoldii* des Abb., 5K 5/7b (BM). Rule = 1 cm.

brown or mottled, naked marginal zone, rhizines long, simple or branched, in scattered groups. Soralia strictly marginal, linear on broad lobes or subcapitate on narrow, lateral lobes. Apothecia rare, stipitate, thalline margin dentate-lobulate or sorediate, disc imperforate, spores (23) 26–32 × 12–15 μm, thick-walled. Pycnidia rare, conidia sublageniform, 7–8 μm long.

TLC: (1) protocetraric acid, ± protolichesterinic acid, ± skyrin, atranorin, (2) protocetraric acid, alectoronic acid, ± skyrin, atranorin, (3) protocetraric acid, α-collatolic acid, ± skyrin, atranorin (rare).

Parmelia subarnoldii represents the sorediate counterpart of *P. amaniensis*, which has the same chemical variation (Table 12). The alectoronic acid strain is most common, while the α-collatolic acid strain is known from only two localities, one in Kenya and one in Uganda.

The species shows great variation in thickness of thallus and length of cilia, but this seems mainly to be a response to the environment. A membranaceous thallus and long cilia are usually associated with shady, moist habitats.

Parmelia subarnoldii grows in fairly well lit sites in coastal hills, inselbergs, and montane forests, between *c.* 500 and 3000 m altitude, but is most common between 1400 and 2400 m. Outside our area it occurs in Malawi and Madagascar (O), and Papua New Guinea (TNS). It has also been recorded from Java, Mexico, and Brazil (Hale, 1965), but with new chemical information these records need verification.

Selected East African records

Kenya. Central Province, Nyeri District, Mt Kenya, W side, Naro Moru track, K 32/107, Aberdare Mts, near Karuru-Gura waterfalls, 3K 32/101; Kirinyaga District, Mt Kenya, S side, Irangi Forest Station, 5K 4/9b; Embu District, Embu, by Izaak Walton Inn, 3K 6/104. Rift Valley Province, Elgeyo Marakwet District, Cherangani Hills 10 km S of Labot, 2K 8/137. Eastern Province, Meru District, Mt Kenya, E side, near Chogoria, 3K 7/108, at Themwe, 3K 16/156; Marsabit District, Mt Marsabit, vicinity of Lake Paradise, 4K 6/140. Coast Province, Kwale District, Shimba Hills, 25 km SW of Mombasa, Makadara Forest, K 43/105. **Tanzania.** Northern Province, Arusha District, Mt Meru Crater, T 5/129; Moshi District, Kilimanjaro, Maua, *Sitari* 670 (TUR). Tanga Province, Lushoto/Tanga District, Usambara Mts, *Holst* 2648 (ZT). **Uganda.** Masaka District, Bukoto County, near Lake Nabugabo, 3U 21/2B, near Kasaka in Jubiya Forest, *Lye* L 607 (herb. Lye); Buddu County, 2 km NW of Bale, Lake Nabugabo, *Lye* L 138A (herb. Lye).

56. Parmelia subcolorata Hale

Contr. U.S. natn. Herb. **36** (5) : 340 (1965).—*Parmotrema subcoloratum* (Hale) Hale, *Phytologia* **28** : 339 (1974). Type: Kenya, Nyanza, Kisumu-Londiani, Tinderet Forest Reserve, 1 August 1949, *R. A. Maas Geesteranus* 5339 (LD, US—isotypes). [TLC: gyrophoric acid, pigment, atranorin.]

Thallus corticolous, loosely attached, pale grey-green. Lobes 1–2 cm broad, crenate, ciliate, cilia 0·5–2 mm long. Upper side emaculate to faintly maculate, distinctly maculate in the vicinity of apothecia, irregularly cracked in central parts. Medulla ochraceous to salmon pink, pigment K−. Underside black with a broad, pale brown marginal zone, rhizines fairly coarse, simple or branched, in scattered patches. Soralia and isidia absent. Apothecia stipitate, thalline exciple rugose, maculate, thalline margin weakly dentate, eciliate or rarely ciliate, disc perforate, spores 13–15 (18) × 8–10 μm long. Conidia filiform, 12–16 μm long.

TLC: gyrophoric acid, pigment, atranorin.

Parmelia subcolorata is here interpreted as the parent morph of *P. permutata.* The partly maculate upper cortex of *P. subcolorata* seems to be associated with the presence of apothecia. Chemical properties are identical, and in both species the gyrophoric acid is concentrated near the upper cortex, giving rise to a colour reaction with C that shades from red in upper parts of the medulla to vivid yellow in lower parts.

The species has been collected in the lower montane forests from 1700 to 2500 m altitude. Unlike the widespread *P. permutata*, it is not known outside the African continent. In addition to the type, Hale (1965) cited a specimen from Zaïre (herb. Degel., not seen).

East African records
Kenya. Coast Province, Taita District, W of Wundanyi, 2K 26/104. Rift Valley Province, Trans-Nzoia District, Mt Elgon, S of Suam River Valley to Kapchaleva Gate, *Ryvarden* 9367b (O); Mt Elgon, E side, *Holm* 11 : 2 (UPS). Nyanza Province, Kisumu-Londiani District, Tinderet Forest Reserve, *Maas Geesteranus* (type collection).

57. **Parmelia subisidiosa** (Müll. Arg.) Dodge

Ann. Mo. bot. Gdn **46** : 87 (1959).—*Parmelia cetrata* var. *subisidiosa* Müll. Arg., *Bot. Jb.* **20** : 256 (1894).—*Parmotrema subisidiosum* (Müll. Arg.) Hale, *Phytologia* **28** : 339 (1974). Type: [Tanzania] Usambara, Bumba, 1894, *Holst* 8772 p. p. (G—holotype). [TLC: salazinic acid, atranorin.]

Thallus corticolous or saxicolous, adnate to loosely attached, pale grey, medium grey, or grey-green. Lobes 0·5–1·2 cm broad, rounded and crenate or irregularly incised and truncate, ciliate, cilia 0·5–2 mm long, sometimes squarrose. Upper side reticulately maculate and cracked. Medulla white. Underside black, with a brown marginal zone, densely rhizinate, rhizines simple, bifurcate, or squarrose, extending almost to the margins. Soralia absent. Isidia laminal and marginal, simple or branched, often bearing cilia, rarely producing lobules or dissolving into granules. Apothecia rare, thalline exciple isidiate, disc imperforate (or perforate), spores 12–14 × 6–10 μm. Conidia filiform, 10–12 μm long.
TLC: salazinic acid, atranorin.

Parmelia subisidiosa is closely related to *P. cetrata* and *P. reticulata*, and may represent the isidiate morph in that species group. We have collected it in montane forests and inselbergs, most commonly between 1800 and 2400 m altitude, with a few isolated finds up to 3200 m. It appears to be a widespread, pantropical to temperate species.

Selected East African records
Ethiopia. Sidamo Province, Gidole, *Winnem* 641/13 (O). **Kenya.** Central Province, Nyeri District, Mt Kenya, W side, K 37/114, 2K 32/103, Aberdare Mts, SE of Lesatima, 5K 13/3; Kirinyaga District, Mt Kenya, S side, vicinity of Irangi Forest Station, K 48/121, Thiba Fishing Camp, K 52/108. Rift Valley Province, Kajiado District, Ngong Hills, K 45/113; Nakuru District, Londiani Forest SE of Mau Summit, 2K 5/1; Kericho District, Kericho Tea Hotel, 4K 15/105. Eastern Province, Meru District, Mt Kenya, E side, at Themwe, 3K 16/68, 127. **Tanzania.** Northern Province, Arusha District, Mt Meru Crater, T 5/139, Arusha National Park, rim of Ngurdoto Crater, T 7/105; Moshi District, Kilimanjaro, Mweka, *Sitari* 289 (TUR). **Uganda.** Ankole District, Igara County, Lubare Ridge, 10 km S of Rubirizi, 2U 3/4.

58. **Parmelia subschimperi** Hale

Phytologia **23** : 345 (1972).—*Parmotrema subschimperi* (Hale) Hale, *Phytologia* **28** : 339 (1974). Type: Kenya, Nanyuki District, Central Province, bamboo zone, National Park road, W slope, Mt Kenya, 2700–3100 m, coll. *R. Santesson* 22150 (UPS—holotype). [TLC: norlobaridone, atranorin.]

Parmelia balensis Winnem, *Norw. J. Bot.* **22** : 151 (1975).—*Parmotrema balense* (Winnem) Hale, *Mycotaxon* **5** : 436 (1977). Type: Ethiopia, Bale Province, mountain pass between Adaba and Goba, 3500–3600 m, coll. *Winnem* 355/28 (O—holotype). [TLC: gyrophoric acid, norlobaridone, atranorin.]

Parmelia neolobulascens Winnem, *Norw. J. Bot.* **22** : 157 (1975).—*Parmotrema neolobulascens* (Winnem) Hale, *Mycotaxon* **5** : 440 (1977). Type: Ethiopia, Semen, Begemder, between Geech and Djinn Bahr, 3400 m, June 1971, coll. *Tapper* 75 (BM—holotype). [TLC: gyrophoric acid, atranorin.]

Parmotrema subcompositum Hale, *Mycotaxon* **5** : 440 (1977). Type: Tanzania, Kilimanjaro [Northern] Province, west slope of Mt Kilimanjaro, east of Lemosho Glades, 2500–2800 m, 14 January 1970, coll. *R. Santesson* 21262 (UPS—holotype). [TLC: gyrophoric acid, norstictic acid, atranorin.]

Thallus corticolous or saxicolous, membranaceous to coriaceous, loosely attached, pale grey to grey-green, margins sometimes tinged with brown. Lobes 1–2 (3) cm broad, rounded,

entire or crenate, ciliate, cilia 0·5–3 mm long, simple or bifurcate. Upper side distinctly maculate, more or less cracked centrally, marginal and laminal lobules occasional. Medulla white. Underside black, with a brown or rarely mottled, naked marginal zone. Rhizines abundant, unevenly distributed. Soralia marginal and submarginal on revolute lobes. Apothecia rare, stipitate or substipitate, thalline exciple sorediate, disc mainly perforate, spores 20–25 (27) × 12–15 (17) μm, relatively thick-walled. Conidia filiform, 12–16 (20) μm long.

TLC: (1) gyrophoric acid, ± norstictic acid, atranorin; (2) norlobaridone, ± norstictic acid, atranorin; (3) gyrophoric acid, norlobaridone, ± norstictic acid, atranorin.

The wide ecological tolerance of *P. subschimperi,* resulting in considerable morphological variation in response to the environment, and the great chemical variation have caused the description of several superfluous species in recent years, here reduced to synonymy. The situation parallels that of its parent morph, *P. euneta* (Table 11).

The species grows to considerable size. In the alpine zone on Mt Kenya we collected a saxicolous specimen measuring nearly 40 cm in diameter.

Parmelia subschimperi is a species of the montane forests and the alpine zone, where we have collected it between 1800 and 3600 m altitude. It is not known outside East Africa.

Selected East African records

Ethiopia. See Winnem (1975) under *P. balensis* pro parte (excluding *P. indoafra*), *P. neolobulascens*, *P. subcomposita*, and *P. subschimperi.* **Kenya.** Central Province, Nyeri District, Mt Kenya, W side, Naro Moru track, several localities, Aberdare Mts, several localities; Kirinyaga District, Mt Kenya, S side, Irangi Forest Station, 5K 4/3. Rift Valley Province, Kajiado District, Ngong Hills, K 45/115; Elgeyo Marakwet District, Cherangani Hills, 10–20 km S of Labot, 2K 7/18, 2K 8/132; Uasin Gishu District, 5 km NW of Timboroa Summit, 2K 19/109, 113; Nakuru District, 1 km S of Mau Narok, 4K 29/107; Laikipia District, Burguret, 4K 25/127. Eastern Province, Meru District, Mt Kenya, E side, at Themwe, 3K 16/194, Mt Kenya, N side, Sirimon track, several localities. **Tanzania.** Northern Province, Arusha District, Mt Meru, several localities, Arusha National Park, near Ngurdoto Gate, T 6/102; Moshi District, Kilimanjaro, W slope, E of Lemosho Glades, *Santesson* 21299a (UPS). **Uganda.** Kigezi District, Bufumbira County, Muhavura, N side, U 16/11. Bugisu District, N Bugisu County, by Sasa Hut on Mt Elgon, 2U 44/36, 0·5 km NW of ford over Sasa River, 2U 45/14.

59. Parmelia subsumpta Nyl.

Flora, Jena **52** : 117 (1869).—*Parmotrema subsumptum* (Nyl.) Hale, *Mycotaxon* **5** : 434 (1977). Type: Brasilia, *Glaziou* 1841 (H–NYL 35451—holotype). [TLC: salazinic acid, undetermined fatty acid, atranorin (+).]

Parmelia leucosemotheta Hue, *Nouv. Archs Mus. Hist. nat., Paris* IV, **1** : 192 (1899).—*Parmotrema leucosemothetum* (Hue) Hale, *Phytologia* **28** : 337 (1974). Type: Mexique, Abredores de san Luis de Potosi, leg. *Paul Maury* (PC—holotype). [TLC: salazinic acid, atranorin (+).]

Parmotrema conferendum Hale, *Mycotaxon* **5** : 433 (1977). Type: Venezuela, Estado de Merida, El Valle, north of Merida, leg. *M. E. Hale* 43,291 (US—holotype). [TLC: norlobaridone, loxodin, atranorin (+).]

Thallus corticolous or saxicolous, coriaceous, loosely attached, grey to pale green. Lobes 0·5–1·5 (2) cm broad, crenate, ciliate, cilia 0·2–2 (3) mm long, coarse or slender, often sparingly developed. Upper side shiny, strongly maculate, cortex irregularly cracked over most of the surface. Medulla white. Underside dark brown to black in the centre, with a broad, brown, mottled, or ivory marginal zone, or underside uniformly pale brown, rhizines dimorphous, in part long, coarse, and penicillate, in part short and slender, covering the lower cortex almost to the lobe margins but sometimes leaving a naked marginal zone. Soralia marginal, linear, becoming crescent-shaped to subcapitate, occasionally spreading on to the lamina on revolute lobes. Apothecia not seen in East African material. (The holotype specimen has perforate apothecia which, according to Winnem (1975), have spores 13 × 8 μm.) Conidia filiform, (10) 12–15 μm long.

TLC: (1) salazinic acid, atranorin (+); (2) norlobaridone, loxodin, atranorin (+).

Parmelia subsumpta belongs to a group of species with a chemical variation involving salazinic acid and norlobaridone (see above under 'Circumscription of the species'); its presumed parent morph is *P. erubescens* (see Table 13). We have found no morphological variation which is correlated with the chemical diversity.

Parmelia leucosemotheta was believed to differ from *P. subsumpta* in its black underside with an erhizinate marginal zone (Hale, 1965). However, the type specimen has a very wide brown zone on the underside, and can be said to be black only in the very centre of the thallus. On the other hand, it does not clearly show the dimorphism of the rhizines in that the short, thin ones, which usually extend to the margins, are largely lacking. Among our specimens from East Africa there is considerable variation in the colour of the underside, and on the same thallus some lobes may be rhizinate or papillate to the margins, while others have a bare marginal zone. The thin, short rhizines are sometimes poorly developed, especially on specimens which have grown on rock, but this trait is not correlated with the colour of the underside. We have found that the various characters intergrade to an extent where a separation into two distinct species becomes impossible.

Only one of our specimens, from Ethiopia (Winnem, 1975, as *P. conferenda*), belonged to the norlobaridone strain, while the rest belonged to the typical strain. The strain corresponding to *Parmotrema reitzii* Hale, with both salazinic acid and norlobaridone, has not yet been found in Africa.

In our area *Parmelia subsumpta* is a species of the lower montane forest where we have collected it on tree trunks and larger branches, more rarely on rock, between 1400 and 2100 m altitude. It has probably been overlooked in Uganda. Outside our area it has been recorded from Zaïre, Transvaal, Natal, and from the Americas (Hale, 1965).

East African records

Ethiopia. Sidamo Province, Yirga Alem, Sidamo Provincial Hospital, E 20/20. For further records, see Winnem (1975). **Kenya.** Western Province, Kakamega District, Kakamega Forest near forest station, *Santesson* 21697 (UPS). Central Province, Kirinyaga District, Mt Kenya, S side, 2 km NW of Irangi Forest Station, near River Ena, K 48/120, near Castle Forest Station, K 49/145, 5K 5/3. Eastern Province, Meru District, near Chogoria, 3K 7/102, Mt Kenya, E side, at Themwe, 3K 16/123, 157. Rift Valley Province, Samburu District, WSW slope of Warges, 4K 3/116; Marsabit District, Mt Marsabit, vicinity of Lake Paradise, 4K 6/142; Laikipia District, Burguret, 4K 25/128. **Tanzania.** Northern Province, Arusha District, Mt Meru, forest on E side, T 10/107, Arusha National Park, Kusare Forest, T 2/111, Juniper Hill, T 3/104, near Ngurdoto Gate, T 6/112, valley by Seneto Pool, T 8/101.

60. Parmelia subtinctoria Zahlbr.

Symb. sin. **3** : 193 (1930).—*Parmotrema subtinctorium* (Zahlbr.) Hale, *Phytologia* **28** : 339 (1974). Type: Sanyingpan, N von Yünnanfu, 2400 m, 14 March 1914, *Handel-Mazetti* 5645 (WU—holotype). [TLC: salazinic acid, norlobaridone, atranorin (+).]

Thallus corticolous, usually membranaceous, loosely attached, grey-green. Lobes 0·5–1.5 cm broad, rounded, crenate, ciliate, cilia 0·2–2 mm long, simple or rarely branched. Upper side distinctly maculate, irregularly cracked. Medulla white. Underside brown to black in the centre, brown marginally, densely rhizinate with a mixture of short and long rhizines, rhizines and papillae often extending to the lobe margins. Soralia absent. Isidia abundant, laminal, thin, simple or branched, rarely ciliate. Apothecia and pycnidia not found in East African material. (According to Hale (1965) the apothecia have imperforate discs and spores 8–11 × 5–8 μm.)

TLC: salazinic acid, norlobaridone, atranorin (+).

Parmelia subtinctoria is closely related to the sorediate *P. subsumpta* (see above), and we expect that it has the same chemical variation (Table 13). We believe that *P. haitiensis* Hale, with only norlobaridone, is conspecific with it, but we have not studied the type of that species.

In East Africa *P. subtinctoria* is a species of well lit sites in the lower montane forest, inselbergs, open hillsides, and roadside trees and gardens between 1300 and 2300 m altitude. It has probably been overlooked in Uganda. Its world distribution has been mapped by Hale (1965, Fig. 24), and it has since been recorded from the Canary Islands by Østhagen & Krog (1976); it is a common and widespread species of tropical and temperate regions.

Selected East African records
Ethiopia. See Winnem (1975). **Kenya.** Central Province, Nyeri District, Mt Kenya, W side, Naro Moru track, K 32/114, Mt Kenya Safari Club, 4K 19/131; Kirinyaga District, Mt Kenya, S side, Thiba Fishing Camp, K 52/107. Rift Valley Province, Narok District, Enabilibil, 22 km S of Siape bridge, 4K 31/106; Kericho District, Kericho Tea Hotel, 4K 16/108; Laikipia District, Naro Moru River Lodge, 2K 34/104, Thomson's Falls, *Santesson* 21970 (UPS); Elgeyo Marakwet District, Sogotio Forest 8 km N of Chebiemit, 2K 10/109; Kajiado District, Ngong Hills, K 45/114; Nakuru District, Londiani Forest SE of Mau Summit, 2K 5/109; Trans Nzoia District, E of Moiben, near Hoey's Bridge, 2K 12/111. Eastern Province, Machakos District, Ol Doinyo Sapuk, 20 km SE of Thika, 2K 2/107; Meru District, Mt Kenya, E side, at Themwe, 3K 16/178; Marsabit District, Mt Marsabit, vicinity of Lake Paradise, 4K 6/141. Western Province, Kakamega District, Kakamega Forest, 0·5 km SW of forest station, 4K 9/114. Nyanza Province, Kisii District, 6 km E of Keroka, 4K 11/110. Coast Province, Taita District, near school W of Wundanyi, 2K 27/117. **Tanzania.** Northern Province, Arusha District, Arusha National Park, Juniper Hill; Moshi District, Kilimanjaro, Lyamungu, Coffee Research Station, *Bigger* 1753 (BM).

61. Parmelia sulphurata Nees & Flotow

Linnaea **9** : (1835).—*Parmotrema sulphuratum* (Nees & Flotow) Hale, *Phytologia* **28** : 339 (1974). Type: Cuba, *Wright* 72 (UPS—neotype, BM—isotype). [TLC: vulpinic acid, atranorin.]

Thallus corticolous, loosely attached, grey-green. Lobes 0·5–1 cm broad, rounded, ciliate, cilia 0·5–1 mm long. Upper side emaculate, irregularly cracked, exposing the pigmented medulla. Medulla intensely sulphur yellow (K−) or orange (K+ purple, skyrin). Underside black, with a mottled, naked marginal zone, rhizines long, sparse, scattered. Soralia absent. Isidia thin, branched, concolorous with the thallus. Apothecia and conidia not found in East African material. (Conidia have been seen in a specimen from Brazil, leg. Malme (O); they were sublageniform, *c.* 5μm long.)

TLC: vulpinic acid, ± skyrin, atranorin.

We have collected *P. sulphurata* only once in East Africa, on a fallen branch in the low coastal hills of Kenya, at 480 m altitude. Its world distribution has been mapped by Hale (1965, Fig. 22). Although largely pantropical, it appears to be very rare in East Africa.

East African record
Kenya. Coast Province, Kwale District, Shimba Hills, 25 km SW of Mombasa, Makadara Forest, K 43/103.

62. Parmelia taitae Krog & Swinscow sp. nov. **Fig. 25**

Thallus saxicola, laxe affixus, griseus. Lobi 1–2 cm lati, orbiculares, marginibus ascendentibus, crenatis, ciliis 0·5–2 mm longis, superne emaculati. Soralia isidiaque nulla. Apothecia submarginalia, ad stipites inflatos, disco ad 2 cm diametro, imperforato. Spori 12–15 (17) × 10 μm. Conidia sublageniformia, 6–8 μm longa. Acidum fumarprotocetraricum, acidum protocetraricum, et atranorinum continens.

Thallus saxicolous, loosely attached, pale grey. Lobes 1–2 cm broad, rounded, lobe margins ascending, crenate, sparingly ciliate, cilia 0·5–2 mm long. Upper side emaculate, slightly shiny. Medulla white. Underside black, with a dark brown, naked marginal zone, rhizines coarse, in scattered groups. Soralia and isidia absent. Apothecia submarginal, stipitate on inflated stipes, thalline exciple smooth, thalline margin dentate, disc up to 2 cm in diameter, imperforate, spores 12–15 (17) × 10 μm. Conidia sublageniform, 6–8 μm long.

TLC: fumarprotocetraric acid, protocetraric acid, atranorin.

Fig. 25 *Parmelia taitae* Krog & Swinscow, holotype (O). Rule = 1 cm.

Type: Kenya, Coast Province, Taita District, Taita Hills, Mt Iyale, 3° 23′ S, 38° 20′ E, alt. 1980 m, epilithic on granitic rock, 9 December 1973, coll. *I. Nordal* no. INB 727 (O—holotype).

Parmelia eborina Hale, described from Central America, has similar spores and conidia but lacks cilia, has subsessile apothecia, and produces protocetraric acid without the addition of fumarprotocetraric acid.

It is possible that *P. taitae* represents the parent morph of *P. pseudograyana*, a sorediate species which occurs in the same general area. They agree in most important characters, but *P. pseudograyana* is a somewhat smaller species with lobes rarely exceeding 1 cm in width.

Parmelia taitae is known only from the type collection and an additional collection, *Nordal* INB 728, from a nearby locality at 2050 m altitude.

63. **Parmelia tinctorum** Despr. ex Nyl.

Flora, Jena **55** : 547 (1872).—*Parmotrema tinctorum* (Despr. ex Nyl.) Hale, *Phytologia* **28** : 339 (1974). Type: Canary Islands, *Despréaux* (?) (H–NYL 35365—holotype). [TLC: not tested.]

Parmelia pseudotinctorum des Abb., *Bull. Inst. fr. Afr. noire* A, **13** : 973 (1951).—*Parmotrema pseudotinctorum* (des Abb.) Hale, *Phytologia* **28** : 338 (1974). Type: Mt Tonkoui, cercle de Man, Ivory Coast, 14 August 1948, *des Abbayes* (US—isotype). [TLC: lecanoric acid, atranorin.]

Thallus corticolous or more rarely saxicolous, membranaceous to coriaceous, loosely attached, pale grey to grey-green. Lobes 1–2 cm broad, rounded, entire or crenate, eciliate. Upper side emaculate, shiny, becoming dull towards the centre, cortex sometimes cracking and flaking. Medulla white. Underside black, with a broad, brown, naked marginal zone, rhizines fairly coarse, in scattered groups. Isidia sparse to abundant, laminal, confluent or in scattered groups, brown tipped or concolorous with the thallus, simple or branched, thin and cylindrical or coarse and irregularly inflated, often interspersed with lobules, sometimes partly or wholly dissolved into granular soredia. Apothecia laminal, substipitate, thalline exciple isidiate, disc dark brown, imperforate or with a small perforation, often radially split, spores 13–15 × 7–8 μm. Conidia filiform, 12–16 μm long.

TLC: lecanoric acid, atranorin.

As mentioned under 'Circumscription of the species' we have found the variation in the vegetative propagules unsuitable for a taxonomic division at species level in this case. There is no difference between *P. tinctorum* and *P. pseudotinctorum* in characters of spores and conidia, perforation of the apothecia, or substrate preference. Both morphotypes have their main distribution between 1000 and 2000 m altitude, with occasional records up to 2700 m, but only *P. tinctorum* s. str. has been found near the coast. None of them occurs in the dry, low lying savanna between *c.* 300 and 900 m.

Parmelia tinctorum is found in mangroves, low coastal hills, and open, well lit upland habitats. It is a common and widespread species of tropical and temperate regions.

Selected East African records

Ethiopia. See Winnem (1975) under *P. tinctorum* and *P. pseudotinctorum.* **Kenya.** Eastern Province, Machakos District, Ol Doinyo Sapuk, 20 km SE of Thika, 2K 2/108, lava flow 5 km NW of Kibwezi, 2K 22/112; Embu District, River Thuchi, south of Chuka, 3K 17/101; Meru District, near Chogoria, 3K 7/106. Rift Valley Province, Kericho District, Kericho Tea Hotel, 4K 16/104; Samburu District, WSW slope of Warges, 4K 3/112; Kajiado District, Chyulu Hills, K 39/101; Laikipia District, Naro Moru River Lodge, 2K 34/105; Marsabit District, Mt Marsabit, vicinity of Lake Paradise, 4K 6/143. Coast Province, Taita District, above Wundanyi, 2K 25/112; Kwale District, Shimba Hills, 25 km SW of Mombasa, Kivumoni Forest, K 41/103, 2 km N of Gazi, in mangrove, K 44/108, 3K 30/154; Kilifi District, Gedi Ruins, 3K 25/103. Western Province, Kakamega District, Kakamega Forest, 0·5 km SW of forest station, 4K 9/109. **Tanzania.** Northern Province, Arusha District, Mt Meru Crater, T 5/152, Arusha National Park, Kusare Forest, T 2/106. Southern Province, Songea District, Gumbiro, *Nordal* INB 849 (O). Southern Highlands Province, Iringa District, Magangwe Ranger Post at Iriki River, *Bjørnstad* AB 1825b (O). Eastern Province, Morogoro District, Morogoro, above university campus,

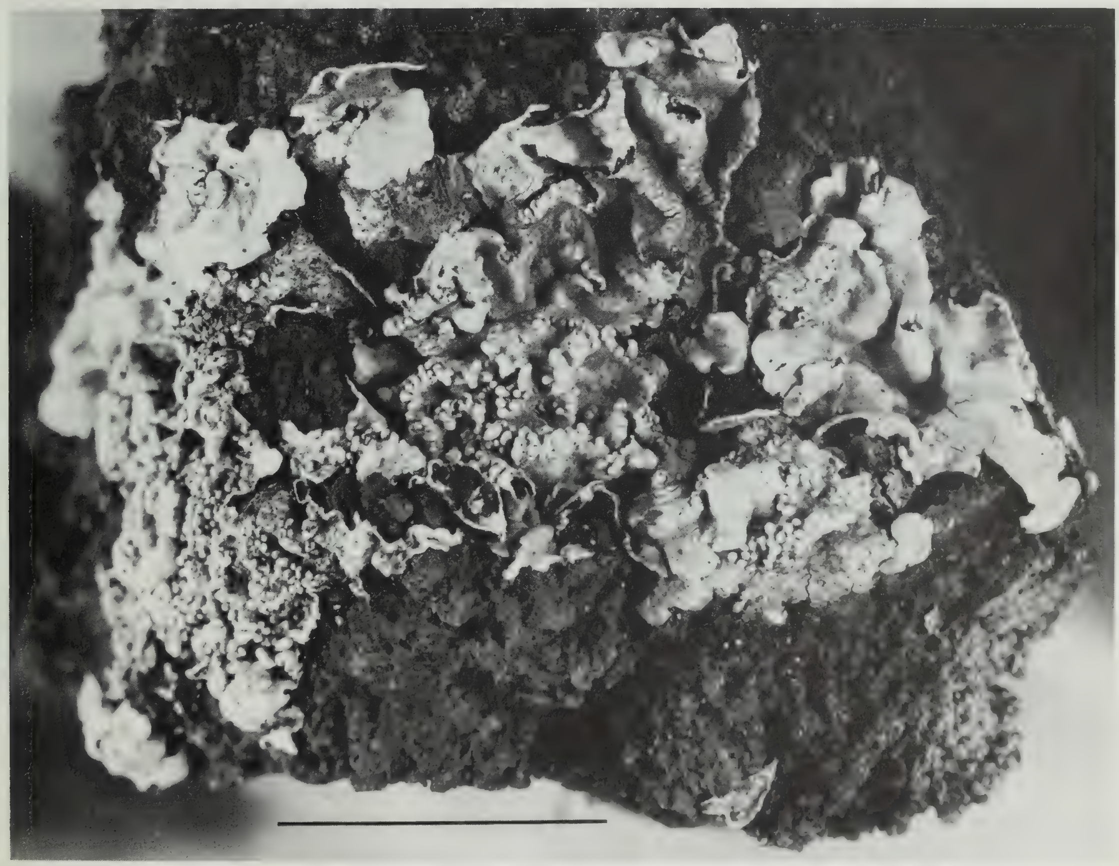

Fig. 26 *Parmelia tsavoensis* Krog & Swinscow, isotype (O). Rule = 1 cm.

30 April 1978, *Dahl* (O). **Uganda.** E. Mengo District, Kyagwe County, Owen Falls Dam, facing Jinja, U 5/4. W. Mengo District, Busiro County, Entebbe Botanical Garden, U 9/1, 68. Kigezi District, Bufumbira County, near Kirwa, Wolfram mine SW of Lake Mutanda, U 22/15a. Karamoja District, Dodoth County, Kidepo Valley National Park, 3U 15/105. Ankole District, Isingiro County, Kikagati, on Kagera River, *Burnet* AMB 201 (BM).

64. Parmelia tsavoensis Krog & Swinscow sp. nov. — Fig. 26

Thallus saxicola, adnatus, griseus. Lobi ad 5 mm lati, eciliati, marginibus integris, superne emaculati, laeves, nitidi. Soralia nulla. Dactyli inaperti, breviter claviformes, ad laminam loborum. Apothecia matura non visa. Conidia filiformia, 18–20 μm longa. Acidum physodicum, acidum oxyphysodicum, et atranorinum continens.

Thallus saxicolous, adnate, pale grey. Lobes up to 5 mm broad, eciliate, with entire margins. Upper side emaculate, smooth, shiny. Medulla white. Underside black, with a broad, brown, naked marginal zone, rhizines short, sparse. Soralia absent. Dactyls closed, shortly claviform, laminally situated towards the centre of the thallus. Mature apothecia not seen. Conidia filiform, 18–20 μm long.

TLC: physodic acid, oxyphysodic acid, atranorin.

Type: Kenya, Eastern Province, Machakos District, lava flow 5 km NW of Kibwezi, 2° 35′ S, 37° 51′ E, on lava rock, 1000 m, January 1972, coll. *H. Krog. & T. D. V. Swinscow* no. K 20/24 (BM—holotype, O, UPS, US—isotypes).

Parmelia tsavoensis recalls forms of *P. stuhlmannii* in its eciliate lobes and closed dactyls resembling coarse isidia, but differs in its longly filiform conidia and in chemical properties.

The species is known only from the type locality, where it was exposed to high light intensity; the black volcanic scoria on which it was growing reached exceedingly high temperatures under the noon sun.

65. Parmlia uberrima Hue — Fig. 27

Mém. Soc. bot. Fr. **28** : 9 (1916).—*Parmotrema uberrimum* (Hue) Hale, *Phytologia* **28** : 339 (1974). Type: Afrique équatoriale anglaise, 1912, leg. *Vicomte de Poncins* (PC—holotype). [TLC: alectoronic acid, atranorin.]

Thallus corticolous, coriaceous, loosely attached, pale grey to green-grey. Lobes 0·5–1·5 cm broad, rounded or irregularly incised, margins ascending, crenate, ciliate, cilia 0·5–2 mm long. Upper side maculate, smooth to rugose or ridged, occasionally with laminal cilia. Medulla white. Underside strongly rugose, black in the centre, with a very broad, white marginal zone, lobe-ends sometimes with small brown patches, rhizines in scattered groups, black, brown, or white, simple or branched, sometimes coalescing into coarse, irregular bundles with penicillate apices. Soralia and isidia absent. Apothecia numerous, submarginal, stipitate, up to 2 cm in diameter, thalline exciple and stipe rugose to strongly reticulately ridged, with coarse, ciliate, isidioid outgrowths often bearing pycnidia, thalline margin ciliate, dentate-lobulate, disc imperforate for a long time, now and then becoming perforate with age, spores (15) 17–20 × (7) 8–10 μm. Conidia shortly filiform, 10–12 μm long.

TLC: alectoronic acid, atranorin.

Parmelia uberrima resembles *P. argentina* Krempelh. in many respects. Both species have small spores, imperforate apothecia with a ciliate thalline margin, a white marginal zone on the underside, and only alectoronic acid in the medulla. The main distinction lies in the coarsely dentate thalline exciple of *P. uberrima*, reminiscent of that found in *P. hanningtoniana*. Conidia were extremely difficult to find in the type material of *P. argentina*, but those seen were rod-shaped and 6–8 μm long. However, they may not have been characteristic of the species, and observations on fresh material are needed to ascertain if this difference is real. If intermediates between *P. uberrima* and *P. argentina* are found, *P.*

Fig. 27 *Parmelia uberrima* Hue, holotype (PC). Rule = 1 cm.

uberrima may be regarded as conspecific with *P. argentina*, but for the time being it seems better to regard them as distinct species.

Parmelia uberrima is mainly a lowland species which has been collected from sea level up to 2000 m altitude; it was locally common on a lava flow in Kenya at 1000 m, where it grew on twigs and thinner branches of shrubs, accompanied by, for example, *P. leonis, P. andina, Dirinaria* spp., and *Ramalina africana.* It seems to prefer well lit, rather dry habitats in scrub, thickets, and miombo woodland. It is so far known only from East Africa.

East African records

Kenya. [? Eastern Province], sine loc., *Poncins* s.n. (PC—holotype). Eastern Province, Machakos District, lava flow 5 km NW of Kibwezi, K 20/121, 2K 22/108, 3K 23/114, 5K 2/27; Kitui District, Mutomo, 50 km NE of Kibwezi, K 21/2. Rift Valley Province, Kajiado District, Chyulu Hills, K 39/5B. Coast Province, Kwale District, 2 km N of Gazi, 3K 30/134. **Tanzania.** Southern Highlands Province, Iringa District, Image Mts., *Nordal* INB 787 (O), Eastern Province, Morogoro District, Mindu Forest Reserve, 4 May 1978, *Dahl* (O). **Uganda.** Masaka District, Bukoto County, 1 km E of Kitakomaga, *Lye* L705 (herb. Lye); Buddu County, near Kirumba, *Lye* L 225 (herb. Lye).

66. Parmelia ultralucens Krog

Bryologist **77** : 253 (1974).—*Parmotrema ultralucens* (Krog) Hale, *Mycotaxon* **1** : 108 (1974). Type: USA, Georgia, Harris Co., Dowdell's Knob, on rock, 1965, *Krog* s.n. (O—holotype). [TLC: salazinic acid, lichexanthone, atranorin.]

Thallus corticolous or saxicolous, loosely attached, pale grey. Lobes 0·8–1·5 cm broad, crenate, ciliate, cilia 0·5–2 mm long. Upper side dull, emaculate, irregularly cracked towards the centre. Medulla white. Underside black, with a broad, brown, naked marginal zone, rhizines dense, of varying length. Soralia absent. Isidia laminal, unevenly distributed, brown tipped, often ciliate. Apothecia and pycnidia not seen in East African specimens. (In extra-African material apothecia are rare, with imperforate discs and spores 15–17 × 10–12μm.)

TLC: salazinic acid, lichexanthone (in the medulla, which reacts UV+ bright yellow), atranorin.

Parmelia ultralucens is the only African *Amphigymnia* species which produces lichexanthone in the medulla.

The species is rare in East Africa; it has been collected twice in the Usambara Mountains in Tanzania at about 900 m altitude. Outside our area it is largely a pantropical to temperate species with its main distribution area in the southeastern US and Central America (Krog, 1974, Fig. 2)

East African records
Tanzania. Tanga Province, Lushoto District, Usambara Mountains, Amani, Dodwe (road towards Derema), *Santesson* 23362 (UPS), Amani, in the surroundings of Forestry House, *Santesson* 23155 (UPS).

67. Parmelia umbrosa Krog & Swinscow sp. nov. **Fig. 28**

Thallus corticola, griseus ad griseo-viridis. Lobi 0·5–1·5 (2) cm lati, orbiculares, integri vel crenati, ciliis 2–4 (5) mm longis, superne nitidi, emaculati, ad centrum irregulariter rimosi. Soralia marginalia, linearia, ad lobos laterales et centrales, raro submarginaliter extensa. Apothecia tantum immatura visa, disco perforato. Conidia filiformia, 10–14 μm longa. Acidum gyrophoricum, acidum protocetraricum, et atranorinum continens.

Thallus corticolous, loosely attached, pale grey to grey-green. Lobes 0·5–1·5 (2) cm broad, rounded, entire or crenate, ciliate, cilia sometimes sparingly developed on peripheral main lobes, usually abundant on lateral and central lobes, 2–4 (5) mm long, simple or branched. Upper side emaculate, irregularly cracked towards the centre. Medulla white. Underside black, with a broad, brown or mottled, naked marginal zone, rhizines abundant, long, slender. Soralia marginal, linear, on lateral and central lobes, occasionally spreading submarginally. Only immature apothecia seen, disc perforate. Conidia filiform, 10–14μm long.

TLC: gyrophoric acid, protocetraric acid, atranorin.

Fig. 28 *Parmelia umbrosa* Krog & Swinscow, holotype (O). Rule = 1 cm.

Type: Kenya. Eastern Province, Meru District, Mt Kenya, E side, near Chogoria, 0° 14′ S, 37° 37′ E, on trees in valley, alt. 1600 m, February 1974, coll. *H. Krog & T. D. V. Swinscow* no. 3K 7/103 (O—holotype, BM—isotype).

Morphologically *P. permutata* may resemble *P. umbrosa* in its emaculate cortex, long cilia, and marginal, linear soralia, but differs in its pigmented medulla and the absence of protocetraric acid. *Parmelia sancti-angelii* differs from *P. umbrosa* in its imperforate apothecia, sublageniform to rod-shaped conidia, and lack of protocetraric acid. *Parmelia indoafra* differs chemically in that it has norlobaridone instead of protocetraric acid, and it also has less well developed cilia.

A combination of protocetraric and gyrophoric acids is known in *Amphigymnia* only from an isotype specimen of the primary species *P. blanchetii* Hue in BM (Winnem, 1975). The type is fragmentary, and it cannot be ascertained if it is related to *P. umbrosa* or not. The protologue mentions that *P. blanchetii* has imperforate apothecia and cylindrical conidia 8–9 μm long, but more material needs to be studied in order to determine whether these differences are real.

Parmelia umbrosa has been collected once in Uganda at *c.* 1300 m altitude and a few times in the lower montane forests on Mount Kenya between 1600 and 2100 m. Outside our area it occurs in Malawi (Southern Province, Mulanje District, Mulanje Mts, Lichenya Plateau, 1800–2000 m, *Ryvarden* 11711, O).

East African records

Kenya. Eastern Province, Meru District, Mt Kenya, E side, near Chogoria, 3K 7/103 (type collection), Mt Kenya, E side, at Themwe, 3K 16/103. Central Province, Kirinyaga District, Mt Kenya, S side, 2 km NW of Irangi Forest Station near River Ena, K 48/134. **Uganda.** Ankole District, Isingiro County, Kikagati, on Kagera River, *Burnet* AMB 201 (BM).

68. Parmelia vivida Krog & Swinscow sp. nov. — Fig. 29

Thallus corticola, coriaceus, adnatus, flavo-viridis. Lobi 0·5–0·8 cm lati, marginibus integris, eciliati, superne emaculati. Soralia isidiaque nulla. Apothecia laminalia, subsessilia, disco imperforato. Spori 20–22 × 8–10 μm. Conidia sublageniformia, 6–7 μm longa. Acidum protocetraricum et acidum usnicum continens.

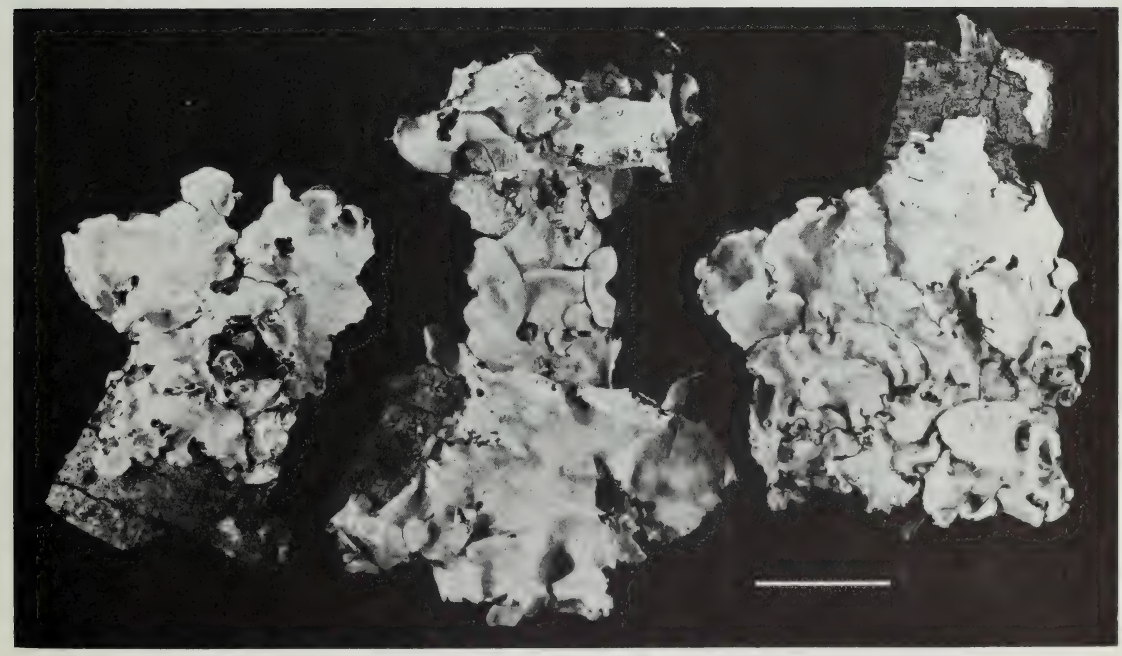

Fig. 29 *Parmelia vivida* Krog & Swinscow, holotype (O). Rule = 1 cm.

Thallus corticolous, coriaceous, adnate, bright yellow-green. Lobes 0·5–0·8 cm broad, rounded, margins entire, eciliate. Upper side matt, emaculate, irregularly cracked towards the centre. Medulla white. Underside black, with a brown, naked marginal zone, rhizines sparse, short. Soralia and isidia absent. Apothecia laminal, subsessile, disc imperforate, spores 20–22 × 8–10 μm. Pycnidia numerous, conidia sublageniform, 6–7 μm long.

TLC: protocetraric acid, usnic acid.

Type: Tanzania, Southern Province, Songea District, Gumbiro, 10° 02′ S, 35° 29′ E, epiphytic in miombo woodland, 920 m, 26 December 1973, coll. *I. Nordal* no. INB 849 (O—holotype).

We consider *P. vivida* to be the parent morph of *P. aprica*, newly described in this work. The species is so far known only from Tanzania.

East African records
Tanzania. Eastern Province, Morogoro District *c.* 20 km SW of Ngerengere, in miombo forest, 1 May 1978, *Dahl* (O, BM). Southern Province, Songea District, Gumbiro, *Nordal* INB 849 (O—type collection).

69. Parmelia xanthina (Müll. Arg.) Vainio

Acta Soc. Fauna Flora fenn. **7** (7) : 37 (1890).—*Parmelia proboscidea* var. *xanthina* Müll. Arg., *Flora, Jena* **67** : 616 (1884).—*Parmotrema xanthinum* (Müll. Arg.) Hale, *Phytologia* **28** : 339 (1974). Type: Central Madagascar, *Hildebrandt* s.n. (G—holotype). [TLC: caperatic acid, undetermined fatty acids, usnic acid, trace atranorin.]

Parmelia nyasensis Dodge, *Ann. Mo. bot. Gdn* **46** : 126 (1959). Type: Mt Nchisi, Nyasaland, *Brass* 16922 (NY—holotype, not seen).

Parmelia aberrans (Vainio) des Abb., *Lichenes Madagascarienses et Borbonici selecti exsiccati (Rennes), fasc. 1, no. 19* (1961).—*Parmelia xanthina* f. *aberrans* Vainio, *Acta Soc. Fauna Flora fenn.* **7**(7) : 37 (1890). Type: Brasilia, Minas Geraës, Sitio, 1000 m, ad truncum arboris, 1885, *E. Vainio* (TUR–VAIN 02758—holotype). [TLC: gyrophoric acid, caperatic acid, undetermined fatty acids, usnic acid, trace atranorin.]

Parmelia madagascariacea (Hue) des Abb., *Lichenes Madagascarienses et Borbonici selecti exsiccati (Rennes), fasc. 1, no. 20* (1961).—*Parmelia caperata* var. *madagascariacea* Hue, *Nouv. Archs Mus. Hist. nat.. Paris* IV, **1** : 18 (1899).—*Parmotrema madagascariaceum* (Hue) Hale, *Phytologia* **28** : 337 (1974). Type: Madagascar, Ambositra, 1889, *Rodriguez* (PC). [TLC: gyrophoric acid aff., caperatic acid, undetermined fatty acids, usnic acid.].

Thallus corticolous (or saxicolous), loosely attached, yellow-green. Lobes 0·5–1 cm broad, crenate, ciliate, cilia 0·3–1 mm long. Upper side dull, emaculate. Medulla white. Underside black, with a brown or mottled, naked marginal zone, rhizines abundant. Soredia absent. Isidia laminal, unevenly distributed, short, thin, brown tipped, abundantly ciliate. Apothecia and pycnidia not seen. (According to Hale (1965) *P. aberrans* has spores 10–16 × 7–10 μm.)

TLC: gyrophoric acid aff., caperatic acid, undetermined fatty acids, usnic acid.

The type specimen of *P. aberrans* gave a C+ rose medullary reaction and undoubtedly contains gyrophoric acid. The East African specimens and the type of *P. madagascariacea* reacted C−, KC+ red; the corresponding spots on the TLC plates went slightly higher in TDA and HEF than those of a gyrophoric acid blank and the substance present in *P. aberrans*. If the negative reaction with C was due to a low concentration of gyrophoric acid, the spots should have been lower rather than higher on the TLC plate. Whatever the difference, the substances in question must be very closely related. The complex fatty acid pattern was the same in all specimens. It included caperatic acid, fatty acids of the reddenda type, and fatty acids with higher Rf values, one of which may coincide with the lower spot produced by protolichesterinic acid. We consider the fatty acids to be diagnostic of the species. The absence of gyrophoric acid or related compounds in *P. xanthina* is here interpreted as depside deficiency of no taxonomic importance.

Hale (1965) regarded *P. xanthina* (including *P. madagascariacea*) and *P. aberrans* as

distinct species on account of the reaction with C in the medulla. Almeda & Dey (1973) considered that all specimens with either a C+ or a KC+ reaction contained gyrophoric acid, and on this basis they found *P. madagascariacea* to be conspecific with *P. aberrans.* They believed that the name *madagascariacea* antedated *aberrans* by a year, a misconception which can be traced back to a printing error in Hale (1965). Des Abbayes (1958) in fact made the two combinations on the same page, but invalidly according to the Code (Art. 33); they were not validated until 1961 (see above under synonyms). [Authors who wish to maintain chemical species within this group should investigate the chemistry of *P. nyasensis* Dodge, which is an earlier name; the KC+ reaction cited by Hale (1965) for this species indicates that the name might take precedence over *P. aberrans* and *P. madagascariacea*.]

Parmelia xanthina is a conspicuous species which is not easily overlooked; it must therefore be regarded as very rare in East Africa. We have collected it once in Kenya, where it grew on trees on an open, well lit hillside at 1500 m altitude. It is common and widespread in the Americas, and has scattered occurrences in Africa and Asia (Hale, 1965).

East African record
Kenya. Eastern Province, Machakos District, Ol Doinyo Sapuk, 20 km SE of Thika, 2K 2/11, 109.

70. Parmelia zollingeri Hepp — Fig. 30

in Zollinger, *Syst. Verz. ind. Archipel* **1** : 9 (1854).—*Parmotrema zollingeri* (Hepp) Hale, *Phytologia* **28** : 339 (1974). Type: In litore pr. Propoli, Prov. Bantam, *Zollinger* 1241 (L—holotype). [TLC: protocetraric acid, atranorin.]

Thallus corticolous, coriaceous, loosely attached, pale grey. Lobes 1–1·5 cm broad, rounded, entire or weakly crenate, eciliate (or with short cilia), central lobes more or less laciniate.

Fig. 30 *Parmelia zollingeri* Hepp, K 44/16 (BM). Rule = 1 cm.

Upper side emaculate, smooth, slightly rugose in older parts. Medulla white. Underside black, with a dark brown marginal zone, rhizines short, sparse, situated in central parts of the thallus. Soralia and isidia absent. Apothecia laminal, cupuliform, shortly stipitate, thalline exciple faintly maculate, disc imperforate, spores 18–22 (24) × 8–10 μm. Conidia sublageniform, 6–8 μm long.

TLC: protocetraric acid, ± fatty acids, atranorin.

All specimens seen from Java, including the types of *P. zollingeri, P. bogoriensis* Zahlbr., and *P. overeemii* Zahlbr., had distinctly ciliate lobe margins, while none of the African specimens showed any tendency towards cilium production. According to Hale (1965) the ciliate margin is a feature mainly of Asian specimens, while those from tropical America lack cilia. This difference is probably of no taxonomic importance.

In East Africa *P. zollingeri* has been found in a broad coastal zone between sea level and *c.* 1000 m altitude, where it grew in mangroves, miombo woodland, on solitary trees in savannas, and at the edge of forests. It is a widespread pantropical species.

East African records

Kenya. Coast Province, Kwale District, 2 km N of Gazi, K 44/16, 3K 30/140, Shimba Hills, 25 km SW of Mombasa, Kivumoni Forest, K 41/105, K 42/103, Shimba Hills, Penga Hill, *Santesson* 20904 (UPS); Kilifi District, Kilifi, *Nattrass* 237 (BM, EA—type collection of *P. litoralis* Dodge). **Tanzania.** Eastern Province, Morogoro District, Nguru ya Ndege, *Pócs & Mwanjabe* 6483/c (herb. Pócs), Mindu Forest Reserve, 4 May 1978, *Dahl* (O), *c.* 20 km SW of Ngerengere, 1 May 1978, *Dahl* (O); Rufiji District, Ngulakula, *Nordal* INB 758 (O). Southern Province, Rungwe District, Mulinda Forest, SE of New Langenberg, *Stolz* 2577 (BM).

71. Parmelia sp. A.

Thallus corticolous, membranaceous, adnate, pale grey. Lobes up to 6 mm broad, rounded and crenate or irregularly incised, eciliate, margins entire or rarely isidiate. Upper side emaculate to faintly maculate, smooth, becoming rugose towards the centre. Medulla white. Underside black, with a broad, brown, naked marginal zone, rhizines few, very short. Isidia numerous, mainly laminally situated, short, slender, simple, concolorous with the thallus. Apothecia and pycnidia not seen.

TLC: protocetraric acid, atranorin.

This species comes closest to *P. adspersa* Vainio, classified in genus *Pseudoparmelia* (=subgenus *Cyclocheila*) by Hale (1976*a*). Morphologically it is very similar to the lectotype and a syntype of that species (TUR–VAIN 02509, 02510), from the Malacca Peninsula in Thailand. However, these specimens, as well as an isotype of *P. filipina* Hale (UPS), reduced by Hale (1976*a*) to synonymy with *P. adspersa*, have a much more complex chemistry. They contain protocetraric acid, fumarprotocetraric acid, two undetermined substances in Rf class 5 in HEF (probably in the protocetraric acid group), and two undetermined fatty acids in Rf class 5 in TA. We agree with Hale in placing *P. filipina* in synonymy with *P. adspersa*, but doubt whether our specimens belong in the same species. The broad, brown, naked marginal zone on the underside of the East African specimens, together with the sparse development of rhizines, indicates subgenus *Amphigymnia*, whereas especially the type specimen of *P. filipina*, which has subsessile, laminal apothecia with spores 10–12 × 8·5 μm, seems to come closer to *Cyclocheila.* More material, preferably fruiting, is needed before the identity of the East African taxon can be settled.

East African records

Kenya. Coast Province, Kilifi District, Gedi ruins, 3K 25/107, Mida Creek, 3K 29/119; Kwale District, 2 km N of Gazi, 3K 30/137.

72. Parmelia sp. B **Fig. 31**

Thallus corticolous, loosely attached, pale grey. Lobes 0·5–1·5 cm broad, rounded or irregularly incised, crenate, ciliate, cilia 0·3–2 mm long. Upper side maculate, cracked and

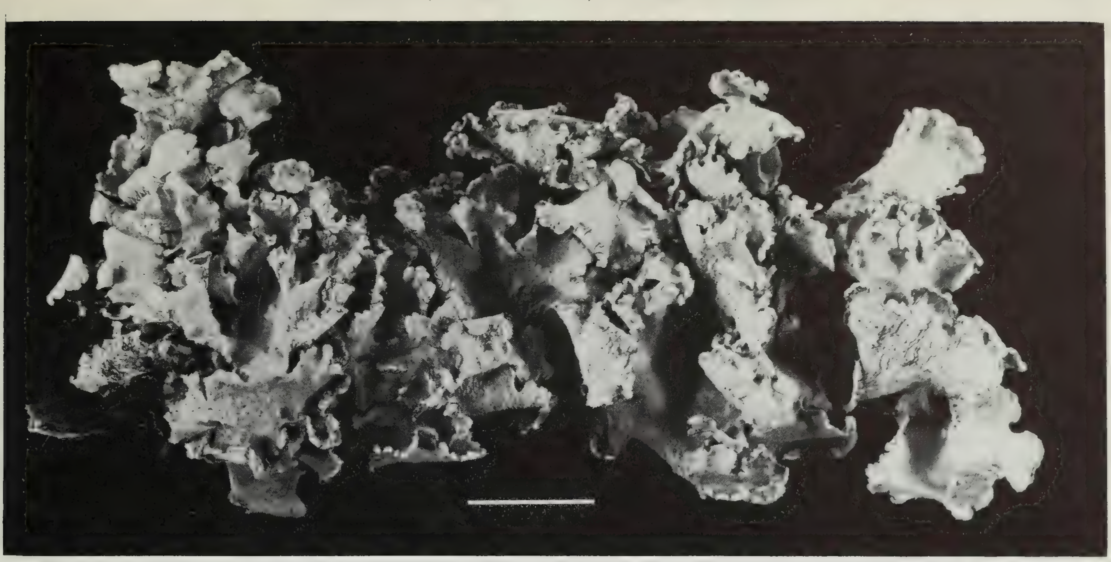

Fig. 31 *Parmelia* sp. B, K 54/109 (O). Rule = 1 cm.

rugose towards the centre. Medulla white. Underside entirely white, rhizines white, black-tipped, or black. Soralia mainly marginal, linear. Apothecia and pycnidia not seen.

TLC: protolichesterinic acid, atranorin.

We believe that 'species B' is the sorediate counterpart of *P. leonis*, newly described in this work. However, in the absence of both apothecia and pycnidia we feel that the relationship is not conclusively proved. At present it is only the entirely white underside that distinguishes our 'species B' from the protolichesterinic acid strain of *P. hababiana*.

'Species B' grew at 1850 m altitude *c.* 130 km north-west of the type locality of *P. leonis*.

East African record

Kenya. Eastern Province, Machakos District, Kilima Kiu, 70 km SE of Nairobi, K 54/109.

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Specific epithets in *Parmelia* (subgenus *Amphigymnia*) and *Parmotrema* are listed. Accepted names are in roman and synonyms in *italic*. New names and principal references are in **bold**, whilst an asterisk (*) denotes a figure.

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The genus *Selaginella* in tropical South America

A. H. G. Alston, A. C. Jermy &
J. M. Rankin

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The genus *Selaginella* in tropical South America

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Prior to his untimely death in 1958, A. H. G. Alston had been preparing an account of the Selaginellas of tropical South America excluding Brazil. Following his death the manuscript lay fallow for a considerable period, but, such was its potential importance in providing an authoritative account by an established specialist of a large and critical genus from a poorly known major region, that my colleagues in the Museum Fern Section, Mr A. C. Jermy and Mr J. A. Crabbe, felt that steps should be taken to make the work available to pteridologists throughout the world. By this time botany had progressed, and considerable revision of the manuscript was essential if the publication was to be more than a fossilised version of the author's intentions and worthy in the 1980s of his international standing in pteridology. The post-Alston additions are clearly indicated in the detailed introduction that follows. I should like to take this opportunity of thanking my colleagues in the Fern Section—Mr A. C. Jermy, Mrs J. M. Rankin and Mr J. A. Crabbe (now retired), for the great amount of careful work that has been put into this publication. While their aim has been solely to make Alston's work as effective as possible for use today, the magnitude and importance of their own contributions, which their reticence partially obscures, should not be overlooked.

J. F. M. Cannon
Keeper of Botany

Contents

Synopsis

This paper completes a series of regional monographs on *Selaginella* written by the late A. H. G. Alston between 1934 and 1955. His manuscript on tropical South American species (excluding Brazilian, for which an account has already been published), was left in an unfinished state in the Department of Botany archives. It has been completed within the style of Alston's accounts, and in order to facilitate the identification of specimens, his account of the Brazilian species has been incorporated.

133 species (and six subspecies or varieties) are keyed out and specimens seen by the authors listed according to geographical location. A table summarises the distribution of all taxa in the states covered by the monograph, namely: Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Surinam and Venezuela.

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The following new taxa are described and illustrated: *Selaginella calceolata* Jermy & Rankin, *S. cheiromorpha* Alston, *S. flacca* Alston, *S. meridensis* Alston, *S. ovifolia* subsp. *philipsonii* Jermy & Rankin, *S. quadrifaria* Alston, *S. sandwithii* Alston, *S. scintillata* Alston, *S. valdepilosa* subsp. *tricholoma* Jermy & Rankin, and *S. wurdackii* Alston. *Selaginella praestans* Alston is a nom. nov. for *S. sprucei* A. Br., non Hook., whilst *S. bahiensis* subsp. *manausensis* (H.P. Bautista) Jermy & Rankin is a new combination.

Somario

Este trabajo completa una serie de monografias regionales sobre *Selaginella* escritas por el difunto A. H. G. Alston entre 1937 y 1955. Su manuscrito sobre especies tropicales sudamericanas (excluyendo las brasileras para las cuales un trabajo ya habia sido publicado) fue depositado, sin completarse, en los archivos del Departamento de Botánica. Ha sido completado al estilo de los trabajos de Alston, pero para facilitar la identificación de especimenes su publicación sobre las especies brasileras también ha sido incorporada.

Ciento treinta y tres especies (y seis subespecies o varidades) son incluídas en la clave y los especimenes vistos por los autores son ordenados en listas de acuerdo con sus localidades geográficas. Una tabla resume la distribución de todos los taxa en los países considerados por la monografiá, siendo estos Bolivia, Brazil, Colombia, Ecuador, Guyana francesca, Guyana, Peru, Surinam y Venezuela.

Los siguientes nuevos taxa son descriptos e illustrados: *Selaginella calceolata* Jermy & Rankin, *S. cheiromorpha* Alston, *S. flacca* Alston, *S. meridensis* Alston, *S, ovifolia* subsp. *philipsonii* Jermy & Rankin, *S. quadrifaria* Alston, *S. sandwithii* Alston, *S. scintillata* Alston, *S. valdepilosa* subsp. *tricholoma* Jermy & Rankin, *S. wurdackii* Alston. Se han hechos los siguientes cambios: *S. praestans* Alston nom. nov. por *S. sprucei* A. Br., non Hook.; *S. bahiensis* subsp. *manausensis* (H.P. Bautista) Jermy & Rankin comb. nov.

Introduction

A. H. G. Alston was, at the time of his unfortunate and sudden death on 17 March 1958, an accredited specialist in the genus *Selaginella.* For almost 30 years he had published regional accounts (see Crabbe, 1960, 1969) with keys, distributional data and synonymy; but rarely, except when describing new species (35 in total), did he describe a taxon in any comparative detail. Mr Alston did not therefore communicate his vast knowledge through his printed works, although the herbarium at the British Museum (Natural History) was curated carefully and shows Alston's ideas on relationships. Nevertheless, his concepts on classification within the genus or his concepts of species (he never used the rank of subspecies, but accepted other workers' varieties) are not at all clear. When pressed for an intra-generic arrangement (e.g. in Walton & Alston, 1938), he followed Baker (1887).

At the time of his death Mr Alston was working on this paper, his last major regional account. He had many years before written an account of the Brazilian species (Alston, 1936) and the paper he was preparing was to cover those tropical countries south of Panama, excluding Brazil. In 1952 he published a revision of West Indies species of *Selaginella* (Alston, 1952), and three years later on those of continental North America, i.e. Panama northwards (Alston, 1955). For all of these works Alston studied the type specimens involved and it may be assumed that the types have been seen unless otherwise stated in this text.

In 1938 he prepared an account for Pulle's *Flora of Suriname* (Alston, 1938), and a year later published (Alston, 1939) an account of the temperate species, i.e. those in Argentina, Uruguay and Paraguay. It was decided that, in order to make this account as comprehensive as possible, the Brazilian data as published in 1936 would be included, but we must stress we have seen little recent material from that country, and appreciate that the distribution of species as shown in Table I therefore may well be changed by the recent collections of H. P. Bautista, A. F. and R. M. Tryon and P. Windische, amongst others. The area now covered is shown on Fig. 1, namely the Guianas, Venezuela, Colombia, Ecuador, Peru, Bolivia and Brazil. A summary of the distribution of the species within these countries is given in Table 1. For the revision, we have not solicited all the material of the past 20 years that must be available, although we have had further material sent by the curators of AAU, CGE, COL, IAN, K, NY, UC, US, VEN. We thank these and the Directors of B, C, E, L, M, P, S, U and

Fig. 1 The area covered by the present account.

UPS and Dr H. P. Bautista (INPA) for sending material when requested and for being tolerant over the time that some of the original material sent to Alston has been kept. Two papers were published (Crabbe & Jermy, 1973, 1976) in order to release loaned material of new species. A further seven new species are published now. All geographical names and provincial boundaries follow *The Times Atlas of the World mid-century edition.* Thus French Guiana records are not divided between the two provinces now maintained in that country, i.e. Cayenne and St Laurent du Maroni.

We should like to record our thanks to Alison Paul (BM) for preparing the map, taking the SEM micrographs and compiling Table 1 and the index, to Dr N. Robson and Miss K. Kavanagh for help with the Latin diagnoses, to Dr S. M. Price for the translation of the synopsis and to J. R. Laundon for editing the manuscript with meticulous care. A special acknowledgement must be made to our former colleague J. A. Crabbe, who had spent much time in organising Alston's manuscript, notes and specimens, and who has prepared an index to collectors, their field numbers and the determination of their material. Due to the cost of production it has been decided not to publish this index but to hold it in the Fern Section library of the British Museum (Natural History). Researchers working on the biography of any botanist involved can write to the Keeper who will place any relevant data at their disposal. We also thank Paul Somers, Jr., for presenting us with his unpublished doctorate thesis (*A systematic survey of the Articulatae series of the genus Selaginella and a monographic treatment of the S. sulcata group* (*sens. str.*) University of Tennessee, Knoxville, 1978). This contains an original approach to *Selaginella* taxonomy. We have with Dr Somers's permission adopted a few nomenclatural changes clarified by him, and look forward to seeing the rest of his researches published in the near future.

Characters used in identification

HABIT. Species of *Selaginella* range from those that are truly prostrate and wide-creeping, through scrambling forms eventually supported by means of 'stilt roots' (rhizophores), to those with various complex forms of branch patterns culminating in dendroid growth forms. Branching patterns are generally of two kinds. In one the whole or primary branch unit is finite in growth, and cones are formed synchronously at all ultimate branch apices. In the other type the lowermost primary branch remains sterile and continues growth only after the upper branches have coned and shed their spores. These two growth patterns were correlated with chromosome base number, the former being based on $2n = 20$ and the latter on $2n = 18$ (Jermy, Jones & Colden, 1967). A further branch system is that in which the main stem is indefinite in growth and the primary branches are finite and often of a distinctive pattern. The outline of branch systems is diagnostic but may be affected by environment. Vegetative reproduction of dendroid species is usually by soboles or stolons. Other species, with a less erect 'frondose' habit and branches showing indeterminate growth, may spread by budding from attenuated (flagelliform) stem apices. Leaves on these extended stems or on the resulting young plants may not be typical in shape, size or density.

STEM. Stem anatomy and the number of vascular bundles have been used by Hieronymus (1901) to demarcate sections within the genus. The latter character has been used in this key and is best examined in main stems. Stem anatomy will repay further study and has been reviewed by Ogura (1972) and Somers (1978). Stems may be deeply suffused with a red pigment (rhodoxanthin; cf. Jagels, 1969). Some species which are lightly tinged pink when fresh lose that colour on drying; in the key, stem colour refers to dried specimens only. Stem 'articulations' (present in species Nos 104–133) are best seen in the dried material as a sunken ring or a dark zone just below the dichotomy forming a branch. Their function, if any, is unknown. Although the tissue organisation of the 'articulations' is not what would be expected of a natural abscission point, Hieronymus (1901) suggests that strong winds, animals or the weight of the plants themselves can break the plants at these points, and Somers (1978) frequently observed specimens broken in this way.

Table 1 Distribution of *Selaginella* species in the countries of tropical South America

		French Guiana	Surinam	Guyana	Venezuela	Colombia	Ecuador	Peru	Bolivia	Brazil
1	*sellowii* Hieron.				●	●	●	●	●	●
2	*sartorii* Hieron.				●	●			●	
3	*peruviana* (Milde) Hieron.						●	●	●	
4	*convoluta* (Arnott) Spring			●	●	●			●	●
5	*pallescens* (C. Presl) Spring				●	●				
6	*erythropus* (Martius) Spring					●	●	●	●	●
7	*umbrosa* Lemaire ex Hieron.					●				
8	*haematodes* (Kunze) Spring				●	●	●	●	●	
9	*coarctata* Spring					●				●
10	*longissima* Baker					●				
11	*mazaruniensis* Jenman			●						
12	*palmiformis* Alston ex Crabbe & Jermy				●	●				
13	*flabellata* var. *latifrons* A. Braun				●					
14	*mortoniana* Crabbe & Jermy					●	●			
15	*lechleri* Hieron.					●		●		
16	*cheiromorpha* Alston					●				
17	*terezoana* Bautista									●
18	*anceps* (C. Presl) C. Presl				●	●	●	●	●	
19	*hirsuta* Alston ex Crabbe & Jermy				●					
20	*bahiensis* Spring subsp. *bahiensis*									●
	subsp. *manausensis* (Bautista) Jermy & Rankin									●
21	*wolfii* Sodiro					●	●	●		
22	*hartii* Hieron.				●					
23	*praestans* Alston					●	●	●		
24	*amazonica* Spring				●	●				●
25	*oaxacana* Spring					●	●			
26	*quadrifaria* Alston					●		●		
27	*tanyclada* Alston ex Crabbe & Jermy					●				
28	*bombycina* Spring					●	●	●		
29	*radiata* (Aublet) Spring	●	●	●		●				●
30	*speciosa* A. Braun					●	●	●		
31	*haenkeana* Spring					●	●	●	●	
32	*hartwegiana* Spring					●	●			
33	*viticulosa* Klotzsch				●	●				
34	*pearcei* Baker				●	●		●		
35	*meridensis* Alston				●					
36	*popayanensis* Hieron.					●	●		●	
37	*cavifolia* A. Braun				●	●	●			
38	*flacca* Alston				●	●				
39	*macilenta* Baker					●	●			
40	*mollis* A. Braun					●				
41	*flagellata* Spring	●	●		●	●	●	●	●	●
42	*moritziana* Spring ex Klotzsch				●		●			
43	*cladorrhizans* A. Braun	●			●	●				●
44	*porphyrospora* A. Braun					●				
45	*novae-hollandiae* (Sw.) Spring				●	●	●		●	
46	*chionoloma* Alston ex Crabbe & Jermy					●		●	●	
47	*lychnuchus* Spring				●	●				

Table 1 *(Continued)*

		French Guiana	Surinam	Guyana	Venezuela	Colombia	Ecuador	Peru	Bolivia	Brazil
48	*ramosissima* Baker						●	●		
49	*glossophylla* Alston ex Crabbe & Jermy								●	
50	*minima* Spring	●								
51	*simplex* Baker				●				●	●
52	*tyleri* A. C. Smith				●					
53	*cruciformis* Alston ex Crabbe & Jermy				●					
54	*acanthostachys* Baker						●	●		
55	*chrysoleuca* Spring				●	●	●	●	●	
56	*contigua* Baker									●
57	*mendoncae* Hieron.									●
58	*leucoloma* Alston ex Crabbe & Jermy								●	
59	*xiphophylla* Baker							●		
60	*substipitata* Spring				●	●				
61	*scalariformis* A. C. Smith				●					
62	*wurdackii* Alston				●					
63	*seemannii* Baker		●			●	●	●		
64	*erectifolia* Spring									●
65	*roraimensis* Baker			●	●					
66	*scintillata* Alston				●					
67	*flexuosa* Spring									●
68	*decomposita* Spring									●
69	*duidae* A. C. Smith				●					
70	*euclimax* Alston ex Crabbe & Jermy					●				
71	*vernicosa* Baker				●					
72	*vestiens* Baker									●
73	*anisoclada* Alston ex Crabbe & Jermy				●	●				
74	*microphylla* (Kunth) Spring				●	●	●	●	●	●
75	*schultesii* Alston ex Crabbe & Jermy					●				
76	*microdonta* A. C. Smith				●					
77	*jungermannioides* (Gaudich.) Spring									●
78	*arenaria* Baker									●
79	*brevifolia* Baker				●	●		●		●
80	*sandwithii* Alston		●	●						
81	*valdepilosa* Baker subsp. *valdepilosa*			●						
	subsp. *tricholoma* Jermy & Rankin			●						
82	*fragillima* Silveira									●
83	*ovifolia* Baker subsp. *philipsonii* Jermy & Rankin					●				
84	*cabrerensis* Hieron.					●				
85	*tuberculata* Spruce ex Baker		●	●						●
86	*rhodostachya* Baker			●	●					
87	*potaroensis* Jenman		●	●	●					
88	*muscosa* Spring			●	●	●		●		●
89	*dendricola* Jenman	●	●	●		●				●
90	*tenuissima* Fée									●
91	*falcata* (Beauv.) Spring	●								
92	*densifolia* Spruce ex Hook.					●				
93	*kochii* Hieron.		●		●	●				●
94	*truncata* Karsten ex A. Braun				●	●		●	●	

Table 1 *(Continued)*

		French Guiana	Surinam	Guyana	Venezuela	Colombia	Ecuador	Peru	Bolivia	Brazil
95	*homaliae* A. Braun					●				●
96	*calosticha* Spring				●			●		
97	*breynii* Spring					●				●
98	*applanata* A. Braun					●		●		
99	*tarapotensis* Baker					●	●	●	●	
100	*producta* Baker	●	●	●	●	●		●		●
101	*macrostachya* (Spring) Spring									●
102	*revoluta* Baker	●	●	●	●	●		●		●
103	*porelloides* (Lam.) Spring	●		●						
104	*exaltata* (Kunze) Spring					●	●	●		●
105	*tomentosa* Spring					●	●			
106	*conduplicata* Spring	●	●			●		●		●
107	*asperula* Spring				●	●		●	●	●
108	*fragilis* A. Braun				●	●				●
109	*parkeri* (Hook. & Grev.) Spring	●	●	●	●	●				●
110	*arthritica* Alston					●	●			
111	*geniculata* (C. Presl) Spring					●	●	●		
112	*dasyloma* Alston					●	●			
113	*anaclasta* Alston ex Crabbe & Jermy				●					
114	*kunzeana* A. Braun				●	●	●	●		
115	*lingulata* Spring					●	●	●	●	
116	*articulata* (Kunze) Spring					●	●	●		
117	*valida* Alston									●
118	*calceolata* Jermy & Rankin					●				●
119	*marginata* (Humb. & Bonpl.) Spring				●				●	●
120	*atirrensis* Hieron.					●		●		
121	*kraussiana* (Kunze) A. Braun									●
122	*asplundii* Alston ex Crabbe & Jermy					●		●		
123	*epirrhizos* Spring	●	●	●						●
124	*poeppigiana* (Spring) Spring ex Splitg.						●	●		
125	*suavis* (Spring) Spring							●		●
126	*silvestris* Asplund					●	●	●	●	
127	*trisulcata* Asplund						●	●	●	●
128	*sericea* A. Braun						●			
129	*sulcata* (Desv.) Spring ex Martius		●						●	●
130	*horizontalis* (C. Presl) Spring				●	●	●			
131	*microtus* A. Braun					●	●			
132	*humboltiana* A. Braun				●	●				
133	*diffusa* (C. Presl) Spring				●	●	●	●	●	

LEAF. In the upper branches of all species, leaves are seen as two kinds: median, on the upper (dorsal) plane of the 'frond', and lateral, on the lower (ventral) side. Those referred to as axillary leaves are modified lateral leaves and occur at all points of dichotomy. They are also of taxonomic value in regard to shape and margin characters.

In dendroid species the leaves on the lower stem are spirally arranged and may not be readily designated medium or lateral. It is a general rule that the shape of both leaf types, but

especially of the median leaves, is narrower near the branch apex, and the assessment of leaf shape should be made from those on primary branches. There is often considerable variation in density and length of cilia on leaves. Somers (1978) points out the importance of uni- or multicellular cilia in species delimitation. The degree of development of leaf auricles is variable. In species with two or more steles, the stems become sulcate on drying and auricles may be hidden in these furrows. The colour of leaves (either a deep or pale green) can be diagnostic. Blue iridescence, which is mainly an optical characteristic of the leaf epidermis, may be found in some species; but its development is usually affected by environmental conditions. The presence of white 'streaks' on leaves is not consistent and of no taxonomic use. The normally clearly defined opaque white borders to both median and lateral leaves are usually significant. The distribution of stomata and of papillae on leaf epidermises (the latter seen clearly in gum-chloral preparations) may prove to be useful diagnostic characters (see Mital, 1969; Bienfait & Waterkeyn, 1974) and needs further investigation. In a few species, the lateral leaves curl under the stems in a characteristic and diagnostic manner, but this feature may not be readily apparent if the specimen was moist when pressed.

Spores. The colour of microspores has been elaborated upon by Hellwig (1969) but is not used here in detail. Somers (1978) found considerable variation within species, and that the colour of microspores may depend on the degree of maturation. These considerations also apply to the colour of megaspores. Sporoderm morphology of both micro- and megaspores is, on the other hand, diagnostic, and has been used by Hieronymus (1901), Hellwig (1969), and Somers (1978). Examination of spores with the scanning electron microscope may show micromorphological differences, but the significance of these can be over-emphasised and so obscure group similarities. However, sporoderm ornamentation can be diagnostic and may be used more usefully as an aid to identification than in this key which is constructed as far as possible for naming sterile material.

Key to species

1a Leaves uniform, spirally arranged . . . . . (subgenus **Selaginella**) 2

1b Leaves dimorphous, at least those on the ultimate branches, in 4 ranks (subgenus **Stachygynadrum**) 4

2a(1) Leafy stems strongly dorsiventral, the zone of green leaves well developed on upper side of stem; leaves on all sides of stem with base decurrent or at least those on underside strongly decurrent; branch tips involute in dormant condition . . . . 3. **peruviana** (p. 251)

2b Leafy stems radially symmetrical; leaves on all sides of stem equal in length, shape, position and texture, with bases abruptly adnate (rarely decurrent on main stem); branch tips not involute in dormant condition 3

3a(2) Leaf-bases glabrous; leaf apex setae usually milk-white, opaque (if whitish to greenish-lutescent and subtranslucent, then setae slightly attenuate) 1. **sellowii** (p. 250)

3b Leaf-bases predominantly pubescent (if, rarely, mostly glabrous, then setae strongly attenuate); leaf apical setae whitish to greenish or lutescent, translucent to subopaque . . . . 2. **sartorii** (p. 251)

4a(1) Rhizophores ventral, i.e. arising on the same side as the axillary leaves; stems not articulate; mega- and microsporophylls the same size 5

4b Rhizophores dorsal, i.e. arising on the opposite side of the stem to the axillary leaves; stems articulate; megasporophylls sometimes much larger than microsporophylls . . . . 129 (p. 248)

5a(4) Stems tufted, curling inwards when dry: leaves rather thick and stiff in texture 6

5b Stems not tufted, not curling when dry; leaves usually membranaceous . . 7

6a(5) Median leaves not margined; texture subcoriaceous; old leaves dark brown 4. **convoluta** (p. 251)

6b	Median leaves white-margined; texture not subcoriaceous; old leaves buff	5. **pallescens** (p. 252)
7a(5)	Stems red or pink	8
7b	Stems stramineous or green	10
8a(7)	Lateral leaves minutely and evenly denticulate on upper margin	8. **haematodes** (p. 254)
8b	Lateral leaves ciliate or ciliolate on upper margin (near base only) . . .	9
9a(8)	Lateral leaves denticulate at apex on both sides, ciliolate at base on upper margin oblong-lanceolate; leaves usually dimorphic before first branch on main stem; median leaves with conspicuous white margin and arista half as long as lamina	6. **erythropus** (p. 253)
9b	Lateral leaves entire throughout the lower margin, long-ciliate at base on upper margin, ovate; leaves usually uniform throughout simple part of main stem; median leaves with narrow white margin, shortly acuminate-aristate	7. **umbrosa** (p. 253)
10a(7)	Plants when fully developed with distinct, usually erect, main stem; leaves ± uniform, appressed at least in lower third	11
10b	Plants with no such distinct and erect stems but usually creeping; leaves for the most part entirely dimorphous throughout the plant	44
11a(10)	Main stem prostrate or arching	12
11b	Main stem erect	13
12a(11)	Stems pubescent, terete; lateral leaves pale green, acuminate .	9. **coarctata** (p. 255)
12b	Stems glabrous, compressed; lateral leaves dark green, subobtuse	10. **longissima** (p. 255)
13a(11)	Main stem compressed	14
13b	Main stem terete	15
14a(13)	Leaves on main stem normally uniform to internode above first branch; lateral leaves deltate to oblong, 4–6 mm long, herbaceous .	11. **mazaruniensis** (p. 255)
14b	Leaves on main stem dimorphous well below first branch; lateral leaves deltate, 3 mm long, subcoriaceous	24. **amazonica** (p. 261)
15a(13)	Leaves on simple part of main stem uniform nearly to first branch, and often to internode above	16
15b	Leaves on simple part of main stem uniform, but becoming dimorphous below the first branch	28
16a(15)	Lateral leaves on the main stem (in the middle of the frond), and on the oldest primary branches ovate-deltate, with a symmetrical apex	17
16b	Lateral leaves on main stem (in the middle of the frond), and on the oldest primary branches oblong, usually with an oblique apex	24
17a(16)	Median leaves broadly elliptic-ovate, densely ciliate at least at base, apex blunt	17. **terezoana** (p. 257)
17b	Median leaves variously shaped, not densely ciliate, apex acuminate to aristate	18
18a(17)	Median leaves distinctly aristate	19
18b	Median leaves acuminate	21
19a(18)	Leaves of main stem obliquely inserted, 3–6 mm long; median leaves long-aristate	14. **mortoniana** (p. 256)
19b	Leaves of main stem above the first branch patent, up to 3 mm long; median leaves shortly aristate	20
20a(19)	Lateral branches mostly regularly pinnate, with simple branchlets; median leaves oblong-ovate, more or less equal-sided, with costa raised; lateral leaves regularly serrate	12. **palmiformis** (p. 256)
20b	Lateral branches mostly bipinnate; median leaves broadly elliptic, with broad outer side; with costa not raised; lateral leaves with few cilia at base, distantly serrate upwards	13. **flabellata** var. **latifrons** (p. 256)

21a(18)	Lateral leaves of branches more than 5 mm long	22
21b	Lateral leaves of branches up to 4 mm long	23
22a(21)	Branch lateral leaves 5 × 2 mm; branch system 2-or-more-pinnate; microspores with elongate papillae . . . . 15. **lechleri** (p.	256)
22b	Branch lateral leaves *c.* 6 × 2·5–3 mm; branch system 1–2-pinnate; microspores smooth . . . . 16. **cheiromorpha** (p.	257)
23a(21)	Lateral leaves glabrous beneath, *c.* 2·5 mm long . . . . . 18. **anceps** (p.	257)
23b	Lateral leaves pubescent beneath, *c.* 4 mm long . . . . . 19. **hirsuta** (p.	259)
24a(16)	Median leaves ± symmetrical, apex acuminate to aristate	25
24b	Median leaves hemi-orbicular, i.e. distictly asymmetrical, apex obtuse or acuminate	27
25a(24)	Branch system ovate or oblong in outline; lateral leaves distinctly dimidiate 21. **wolfii** (p.	260)
25b	Branch system pedate in outline; lateral leaves not markedly dimidiate . .	26
26a(25)	Median leaves obovate-elliptic, dentate, apex acuminate often into a short arista 20. **bahiensis** subsp. **bahiensis** (p.	259)
26b	Median leaves lanceolate-elliptic, denticulate, apex acute 20. **bahiensis** subsp. **manausensis** (p.	260)
27a(24)	Median leaves sparingly ciliate at base, apex obtuse; lateral leaves 7–8 mm 23. **praestans** (p.	260)
27b	Median leaves denticulate at base, apex acute; lateral leaves rarely more than 5 mm 25. **oaxacana** (p.	261)
28a(15)	Largest lateral leaves 6–10 mm long	29
28b	Largest lateral leaves 3–4 mm long	35
29a(28)	Lateral leaves ciliate at base; lateral leaves of secondary and tertiary branches about equal	30
29b	Lateral leaves denticulate at base; lateral leaves of secondary and tertiary branches equal or unequal	33
30a(29)	Median leaves not aristate, at most slightly acuminate	31
30b	Median leaves aristate	32
31a(30)	Costa of median leaves not central; abaxial part of lamina twice as broad as adaxial part . . . . 23. **praestans** (p.	260)
31b	Costa of median leaves nearly central; abaxial part of lamina not twice as broad as adaxial part . . . . 26. **quadrifaria** (p.	261)
32a(30)	Median leaves longer than broad, ± asymmetrical, tapering gradually into a short arista . . . . 27. **tanyclada** (p.	263)
32b	Median leaves broader than long, strongly asymmetrical, abruptly acuminate with a ± long arista . . . . 28. **bombycina** (p.	264)
33a(29)	Lateral leaves of secondary and tertiary branches about the same size 30. **speciosa** (p.	265)
33b	Lateral leaves of tertiary branches much smaller than those of secondary branches	34
34a(33)	Lateral leaves of upper part of main stem with conspicuous anterior basal lobe often overlapping stem; median leaves ± symmetrical, shortly aristate 21. **wolfii** (p.	260)
34b	Lateral leaves of upper part of main stem without conspicuous anterior basal lobe; median leaves distinctly asymmetrical with long arista . 22. **hartii** (p.	260)
35a(28)	Lateral leaves of main stem subcoriaceous, imbricate, denticulate 24. **amazonica** (p.	261)
35b	Lateral leaves of main stem herbaceous, imbricate or not, denticulate to ciliate	36
36a(35)	Lateral leaves ciliate at base	37
36b	Lateral leaves denticulate at base	41

37a(35) Lateral leaves ovate with cilia evenly spaced, uniform; microspores papillose 33. **viticulosa** (p. 266)
37b Lateral leaves ovate-oblong or lanceolate with cilia irregular in length and spacing; microspores papillose or not 38

38a(37) Median leaves of main stem distinctly asymmetrical, with an obtuse apex abruptly forming an arista ± as long as the leaf-blade . 31. **haenkeana** (p. 265)
38b Median leaves of main stem ± symmetrical, with an acute apex tapering to a arista $< \frac{2}{3}$ length of leaf-blade 39

39a(38) Median leaves with a short arista and large outer auricles; with no, or few, cilia at base; axillary leaves narrowly deltate or deltate-ovate; microspores smooth 32. **hartwegiana** (p. 266)
39b Median leaves with an arista about half as long as leaf-blade, outer auricle virtually absent, ± densely ciliate at base; axillary leaves lanceolate; microspores papillate 40

40a(39) Lateral leaves 3–4 mm long, upper margin toothed with few short cilia at base 35. **meridensis** (p. 267)
40b Lateral leaves 0·5–2 mm long, upper margins with long, often dense, cilia 29. **radiata** (p. 264)

41a(36) Median leaves aristate . . . . 35. **meridensis** (p. 267)
41b Median leaves not aristate 42

42a(41) Branch system caulescent, main stem 1·5–2 mm thick; lateral leaves overlapping 24. **amazonica** (p. 261)
42b Branch system diffuse, main stem not more than 1 mm thick; lateral leaves distant 43

43a(42) Median leaves broadly ovate to elliptic, obtuse with small acumen; lateral leaves oblong-elliptic . . . . 34. **pearcei** (p. 267)
43b Median leaves lanceolate-elliptic, acute or shortly acuminate; lateral leaves broadly ovate-elliptic . . . . 36. **popayanensis** (p. 269)

44a(10) At least some stems and/or branches with flagelliform apices, or plants soboliferous 45
44b Stems and/or branches without flagelliform apices; plants not soboliferous . 58

45a(44) Mature stems rather stout, about 1·5 mm in diameter . . 10. **longissima** (p. 255)
45b Mature stems slender, up to 1 mm in diameter 46

46a(45) Plant truly creeping, main stems bearing rhizophores above lower third . . 47
46b Plant tending to be erect or upper branches ascending, main stems usually without rhizophores above lower third 52

47a(46) Lateral leaves strongly ciliate, at least in lower half . . . 40. **mollis** (p. 272)
47b Lateral leaves not more than denticulate (occasionally with a few short cilia on auricles) 48

48a(47) Lateral leaves up to twice as long as broad; median leaves usually aristate 41. **flagellata** (p. 272)
48b Lateral leaves not more than 1·5 times as long as broad; median leaves rarely aristate 49

49a(48) Median leaves cordate at base, nearly as broad as long, subacute; lateral leaves rounded at apex . . . . 76. **microdonta** (p. 288)
49b Median leaves not cordate at base, 1·5 times as long as broad, acute to acuminate or shortly aristate; lateral leaves acute or acuminate 50

50a(49) Median leaves acute or shortly and abruptly acuminate, entire or finely toothed, not papillate . . . . 37. **cavifolia** (p. 269)
50b Median leaves acuminate-aristate, often coarsely toothed, surface papillate . 51

51a(50) Lateral leaves broadly ovate with an acuminate apex . . . 38. **flacca** (p. 269)
51b Lateral leaves lanceolate-elliptic, apex acute . . . . 39. **macilenta** (p. 272)

52a(46) Lateral leaves acuminate to aristate; median leaves ciliate 54. **acanthostachys** (p. 278)

52b	Lateral leaves not aristate; median leaves not ciliate, although with occasional long teeth in upper part	53
53a(52)	Median leaves not auriculate; lateral branches with flagelliform apices; basal soboles not present	54
53b	Median leaves auriculate; lateral branches rarely with flagelliform apices (*acanthostachys*); basal soboles usually present	55
54a(53)	Lateral leaves ovate, usually with short hairs on basiscopic side of upper surface and with two false nerves; megaspores orange	44. **porphyrospora** (p. 274)
54b	Lateral leaves linear-lanceolate or oblong, glabrous and with a single nerve; megaspores pale cream	43. **cladorrhizans** (p. 274)
55a(53)	Median leaves not bordered, finely denticulate	42. **moritziana** (p. 273)
55b	Median leaves distinctly white- or hyaline-bordered, dentate to often spinose-toothed or ciliate	56
56a(55)	Leaves spinose-dentate but not ciliate, lateral leaves with conspicuous white border often 2–3 cells broad on acroscopic margin, drying ± flat	46. **chionoloma** (p. 276)
56b	Leaves ciliate on acroscopic margin, with narrow ± hyaline border, curling when dry	57
57a(56)	Upper lateral leaves acuminate to aristate; median leaves with long white arista	54. **acanthostachys** (p. 278)
57b	Upper lateral leaves at the most only apiculate; median leaves without white arista	45. **novae-hollandiae** (p. 274)
58a(44)	Main stems usually suberect without rhizophores above lower third	59
58b	Main stems prostrate with rhizophores above the lower third	94
59(58)	Sporophylls strongly dimorphous	60
59b	Sporophylls uniform or nearly so	65
60a(59)	Lateral leaves obtuse, oblong	61
60b	Lateral leaves acute, variable in shape	63
61a(60)	Lateral leaves ciliolate or ciliate at base	47. **lychnuchus** (p. 276)
61b	Lateral leaves denticulate at base	62
62a(61)	Stem 1 mm in diameter at base; lateral leaves broadest below middle, more than twice as long as broad	48. **ramosissima** (p. 277)
62b	Stem filiform, i.e. less than 1 mm diameter throughout; lateral leaves broadest above middle, up to twice as long as broad	49. **glossophylla** (p. 277)
63a(60)	Median leaves long-aristate; lateral leaves with distinct white border	46. **chionoloma** (p. 276)
63b	Median leaves acute to acuminate; lateral leaves not bordered	64
64a(63)	Lateral leaves oblong, ciliate; lower sporophylls ciliate	50. **minima** (p. 277)
64b	Lateral leaves ovate, denticulate; lower sporophylls denticulate	51. **simplex** (p. 277)
65a(59)	Lateral leaves densely pubescent on both surfaces or shortly so on upper surface of lower half	66
65b	Leaves glabrous on both surfaces	67
66a(65)	Both median and lateral leaves with long hairs on surface and on margins as cilia; lateral leaves with single nerve	52. **tyleri** (p. 277)
66b	Median leaves glabrous, lateral leaves with short hairs on basiscopic side of upper surface only; lateral leaves with two false nerves	44. **porphyrospora** (p. 274)
67a(65)	Stems 10–15 mm across (including leaves)	68
67b	Stems less than 8 mm across (including leaves)	71
68a(67)	Median leaves subacute	53. **cruciformis** (p. 278)
68b	Median leaves acuminate to aristate	69

69a(68)	Median leaves finely toothed, without cilia	55. **chrysoleuca** (p. 278)
69b	Median leaves ciliate	70
70a(69)	Median leaves with a distinct arista	56. **contigua** (p. 278)
70b	Median leaves acuminate	57. **mendoncae** (p. 279)
71a(67)	Median leaves ciliate at least in the lower half	72
71b	Median leaves not ciliate (although sometimes sharply toothed)	74
72a(71)	Sporophylls acuminate, ciliate throughout margin; leaves dark green; lateral leaves ovate, symmetrical	54. **acanthostachys** (p. 278)
72b	Sporophylls subacute, toothed, sometimes ciliate at base; leaves light green; lateral leaves asymmetrical	73
73a(72)	Median leaves subacute	58. **leucoloma** (p. 279)
73b	Median leaves aristate or abruptly acuminate	45. **novae-hollandiae** (p. 274)
74a(71)	Lateral leaves oblong-lanceolate, more than twice as long as broad, apex obtuse; stems not filiform, usually more than 0·5 mm in diameter	75
74b	Lateral leaves ovate deltate to broadly lanceolate, up to 1·5 times as long as broad, apex acute; stems filiform, up to 0·25 mm in diameter (except *S. pearcei*)	87
75a	Arista of median leaves more than half as long as lamina	76
75b	Arista of median leaves up to a third as long as lamina, or wanting, or leaves acuminate	77
76a	Lateral leaves closely and regularly spaced, dark green	59. **xiphophylla** (p. 279)
76b	Lateral leaves distant, light green	60. **substipitata** (p. 279)
77a	Lateral leaves distinctly white-margined	84. **cabrerenis** (p. 294)
77b	Lateral leaves not white-margined	78
78a(77)	Lateral leaves transversely disposed in opposite plane to stem; median leaves elliptic-orbicular, closely ciliolate	61. **scalariformis** (p. 280)
78b	Lateral leaves not as above; median leaves oblong-ovate to obovate or narrowly elliptical, dentate	79
79a(78)	Sporophylls lanceolate-deltate	80
79b	Sporophylls ovate-deltate	82
80a(79)	Stems slender, 0·5 mm in diameter; lateral leaves ± entire	62. **wurdackii** (p. 280)
80b	Stems stout, 1 mm in diameter; lateral leaves ciliate or toothed	81
81a(80)	Median leaves oblong-lanceolate, acuminate with short hyaline tip; lateral leaves 2–3 mm long, patent even when dry	63. **seemannii** (p. 280)
81b	Median leaves ovate-elliptic, acuminate into arista; lateral leaves 1–2 mm long, especially the lower ones erect and clasping the stem	64. **erectifolia** (p. 282)
82a(79)	Median leaves acute	83
82b	Median leaves acuminate or aristate	84
83a(82)	Lateral leaves *c.* 1 mm long; rhizophores short and filiform	66. **scintillata** (p. 282)
83b	Lateral leaves *c.* 2 mm long; rhizophores long and stiff	65. **roraimensis** (p. 282)
84a(82)	Main stem (incl. lateral leaves) 8–10 mm wide; lateral leaves entire	67. **flexuosa** (p. 282)
84b	Main stem (incl. lateral leaves) < 5 mm wide, or if wider then lateral leaves wide-spaced; lateral leaves denticulate at least on acroscopic edge	85
85a(84)	Lateral leaves on main branches distant, with hyaline teeth on both margins	68. **decomposita** (p. 285)
85b	Lateral leaves on main branches closely set, with teeth only on acroscopic margin	86
86a(85)	Median leaves abruptly acuminate into short, ± hyaline arista; lateral leaves dentate towards acute apex	69. **duidae** (p. 286)
86b	Median leaves acuminate; lateral leaves with distinct teeth only at base, apex obtuse	70. **euclimax** (p. 286)
87a(74)	Surface of leaves polished and texture firm	88

87b	Surface of leaves not polished and/or texture somewhat diaphanous . . .	91
88a(87)	Lateral leaves all overlapping; lateral branches usually ascending 71. **vernicosa** (p.	286)
88b	Lateral leaves spaced towards base of stem	89
89a(88)	Lateral branches ascending . . . . 66. **scintillata** (p.	282)
89b	Lateral branches usually spreading at an angle of 45 degrees	90
90a(89)	Lateral leaves ovate, ± entire; median leaves subacute 86. **rhodostachya** (p.	296)
90b	Lateral leaves broadly lanceolate, ciliatodentate; median leaves acuminate 72. **vestiens** (p.	286)
91a(87)	Lateral leaves of main stem very distant and much longer than those of branches 73. **anisoclada** (p.	287)
91b	Lateral leaves of main stem less than one leaf's length apart, not much longer than those of largest branches	92
92a(91)	Lateral leaves ovate-deltate, distinctly asymmetrical . . 80. **sandwithii** (p.	289)
92b	Lateral leaves ovate-lanceolate to elliptic, ± symmetrical	93
93a(92)	Median leaves lanceolate-elliptic, acute or shortly acuminate; lateral leaves broadly ovate-elliptic . . . . 36. **popayanensis** (p.	269)
93b	Median leaves broadly ovate-elliptic, obtuse but with acute acumen; lateral leaves oblong-elliptic . . . . 34. **pearcei** (p.	267)
94a(58)	Lateral and axillary leaves ovate, up to twice as long as broad	95
94b	Lateral and axillary leaves oblong, usually more than twice as long as broad .	114
95a(94)	Lateral leaves ciliate at base	96
95b	Lateral leaves denticulate	104
96a(95)	Lateral leaves inserted obliquely, clasping the stem when dry; median leaves similar to lateral leaves suborbicular, subacute . . . 74. **microphylla** (p.	287)
96b	Lateral leaves patent, often rolling under from apex to base when dry; median leaves different from the lateral leaves broadly elliptic to ovate-lanceolate, subacute to apiculate	97
97a(96)	Median leaves aristate, acuminate or cuspidate; lateral leaves acute or obtuse .	98
97b	Median leaves not aristate or acuminate or cuspidate; lateral leaves obtuse .	101
98a(97)	Median leaves with long aristate tip; lateral leaves *c.* 1 mm long 75. **schultesii** (p.	288)
98b	Median leaves acuminate or cuspidate; lateral leaves 1·5–3·0 mm long . .	99
99a(98)	Width of stem plus lateral leaves 3–4 mm; secondary branches unbranched; rhizophores throughout main stem . . . 77. **jungermannioides** (p.	288)
99b	Width of stem plus lateral leaves 2·0–2·5 mm; secondary branches mostly dichotomous; rhizophores in lower third of main stem only	100
100a(99)	Lateral leaves often densely ciliate on both margins, at least below; median leaves broadly elliptic, not acuminate . . . . . . 78. **arenaria** (p.	289)
100b	Lateral leaves sparsely ciliate on acroscopic margin, basiscopic margin ± entire; median leaves ovate-elliptic, acuminate . . . . 79. **brevifolia** (p.	289)
101a(97)	Median leaves suborbicular, ciliate	102
101b	Median leaves lanceolate or oblong-elliptic, not ciliate (or occasionally so at apex)	103
102a(101)	Lateral leaves 1·5 times as long as broad, contiguous 81. **valdepilosa** subsp. **valdepilosa** (p.	292)
102b	Lateral leaves twice as long as broad, not contiguous 81. **valdepilosa** subsp. **tricholoma** (p.	292)
103a(101)	Median leaves lanceolate with distinct white border, without apical setae 82. **fragillima** (p.	294)
103b	Median leaves oblong-elliptic without white border, with 2–3 apical setae 83. **ovifolia** subsp. **philipsonii** (p.	294)
104a(95)	Median leaves subacute, neither aristate or acuminate	105

104b Median leaves acuminate or aristate 108

105a(104) Upper surface of lateral leaves beset with tubercles near the lower margin 85. **tuberculata** (p. 296)
105b Upper surface of lateral leaves smooth 106

106a(105) Lateral leaves costate to apex . . . . 86. **rhodostachya** (p. 296)
106b Lateral leaves ecostate, or costate at base only 107

107a(106) Median leaves deltate-orbicular . . . . . . 76. **microdonta** (p. 288)
107b Median leaves ovate-oblong . . . . 37. **cavifolia** (p. 269)

108a(104) Median leaves (exclusive of the apical cusp) less than half as long as lateral leaves, outer side cordate . . . . 87. **potaroensis** (p. 297)
108b Median leaves (exclusive of the apical cusp) more than half as long as lateral leaves, outer side rounded or auricled 109

109a(108) Sporophylls uniform or nearly so; median leaves aristate 110
109b Sporophylls dimorphous; median leaves acute to shortly aristate . . . 112

110a(109) Lateral leaves ovate to ovato-deltate, 2·5–3 mm long, apex becoming acute 88. **muscosa** (p. 297)
110b Lateral leaves of main stem ovato-suborbicular, *c.* 1 mm long, apex rounded obtuse (those on fertile branches may be ovate-elliptic and <2 mm long) . 111

111a(110) Lateral leaves heteromorphous (i.e. some larger and closer than others); median leaves ovate-elliptic, apex acute . . . . . . 89. **dendricola** (p. 299)
111b Lateral leaves not heteromorphous; median leaves suborbicular-elliptic, apex aristate 90. **tenuissima** (p. 299)

112a(109) Lateral leaves obtuse or subacute, strongly cordate at base on upper side only 103. **porelloides** (p. 305)
112b Lateral leaves acute or acuminate, rounded at base 113

113a(112) Sporophylls ovate; median leaves acuminate . . . . . 37. **cavifolia** (p. 269)
113b Sporophylls lanceolate; median leaves shortly aristate . . . 38. **flacca** (p. 269)

114a(94) Lateral leaves with hyaline margin of three or more rows of elongate cells on both sides of the leaf 115
114b Lateral leaves with no hyaline margin; marginal cells on lower side of leaf near apex quadrate, or, if elongate, then cells with chloroplasts 118

115a(114) Median leaves ovate or ovate-deltate, acute-acuminate, falcate 116
115b Median leaves oblong-lanceolate, aristate, not falcate 117

116a(115) Median leaves acuminate, ciliate for 2/3 of margin, apices pointing outwards; lateral leaves ciliate at base . . . . 91. **falcata** (p. 300)
116b Median leaves acute, ciliate on auricles only, apices pointing inwards; lateral leaves with at most a few cilia at base . . . . . 92. **densifolia** (p. 300)

117a(115) Stems (including leaves) up to 3·5 mm across, ascending, with short often slender rhizophores; lateral leaves densely ciliate, ensheathing stem when dry 84. **cabrerensis** (p. 294)
117b Stems (including leaves) normally 6 mm or more across, prostrate, with long stout rhizophores; lateral leaves spinose-dentate, becoming ciliolate on auricles, not curling round stem when dry . . . . 93. **kochii** (p. 301)

118a(114) Median leaves subacute or at most slightly cuspidate 119
118b Median leaves aristate 120

119a(118) Stems (including leaves) 6–8 mm across; leaves sparsely and minutely toothed 94. **truncata** (p. 301)
119b Stems (including leaves) up to 3·5 mm across; leaves spinose-toothed 95. **homaliae** (p. 302)

120a(118) Median leaves conspicuously white-margined 121

120b	Median leaves not conspicuously white-margined	124
121a(120)	Lateral leaves not ciliate	122
121b	Lateral leaves ciliate	123
122a(121)	Median leaves ovate-lanceolate, gradually attenuate into a long arista which equals lamina . . . . 59. **xiphophylla** (p.	279)
122b	Median leaves broadly oblong, abruptly attenuate, arista shorter than lamina 96. **calosticha** (p.	302)
123a(121)	Stems (including leaves) 7 mm or more across; microspores with capitate verrucae 97. **breynii** (p.	302)
123b	Stems (including leaves) up to 5 mm across; microspores with elongate papillae 98. **applanata** (p.	303)
124a(120)	Microspores with stalked papillae; arista of median leaves ± equalling lamina	125
124b	Microspores smooth; arista of median leaves not more than half lamina . .	126
125a(124)	Lateral leaves ovate-elliptic, twice as long as broad . . 99. **tarapotensis** (p.	303)
125b	Lateral leaves oblong-elliptic, about three times as long as broad 67. **flexuosa** (p.	282)
126a(124)	Lateral leaves denticulate, cilia if present confined to auricles, subobtuse, drying flat	127
126b	Lateral leaves ciliate, subacute, often longitudinally inrolled	128
127a(126)	Branches usually short and simple; lateral leaves 2–3 mm long, not uniform in length and more distant in some parts of the stem; leaf texture membranous 89. **dendricola** (p.	299)
127b	Branches usually pinnate; lateral leaves 3–4 mm long, uniform in both length and distribution; leaf texture firm . . . . . . 100. **producta** (p.	303)
128a(126)	Secondary branch units 4–10 cm, 3–4 times forked . 101. **macrostachya** (p.	304)
128b	Secondary branch units 1–2 cm, 1–2 times forked . . . 102. **revoluta** (p.	304)
129a(4)	Branches pubescent (main stems sometimes glabrescent)	130
129b	Branches glabrous	132
130a(129)	Leaves of main stem spreading, rather close, obtuse . . 116. **articulata** (p.	313)
130b	Leaves of main stem directed upwards, distant, acute	131
131a(130)	Stem scandent with spreading, bipinnate, frond-like branches 104. **exaltata** (p.	306)
131b	Stem erect with an apical 3–4-pinnate frond-like portion . 105. **tomentosa** (p.	306)
132a(129)	Main stems simple, erect, with leaves subequal towards the base; lateral leaves appressed to stem	133
132b	Main stems branched from the base, prostrate or rarely ascending; with leaves dimorphous throughout; lateral leaves spreading	138
133a(132)	Axillary leaves with long spur-like auricles . . . 106. **conduplicata** (p.	306)
133b	Axillary leaves exauriculate or with very short auricles	134
134a(133)	Main stems with one stele	135
134b	Main stems with two steles	137
135a(134)	Primary branch width (incl. leaves) 3–4 mm . . . . 107. **asperula** (p.	307)
135b	Primary branch width (incl. leaves) 5–7 mm	136
136a(135)	All aerial stems determinate, not rooting at apex . . . 109. **parkeri** (p.	309)
136b	Main and primary branch stems indeterminate, usually rooting at apex 108. **fragilis** (p.	308)
137a(134)	Lateral leaves up to 2 mm broad, with a triangular auricle on lower side; outer auricles on median leaves usually rounded . . . . 111. **geniculata** (p.	310)
137b	Lateral leaves up to 3·5 mm broad, rounded or truncate on lower side at base; outer auricle on median leaves usually distinctly angular . 110. **arthritica** (p.	310)
138a(132)	Median leaves obtuse, fringed with spreading hairs . . 112. **dasyloma** (p.	311)
138b	Median leaves acute, acuminate or aristate, not fringed with spreading hairs .	139

139a(138) Median leaves aristate, fringed with stiff spreading teeth, tipped by cilia; branches recurved . . . . 113. **anaclasta** (p. 312)
139b Median leaves variable but with cilia at base only or wanting; branches not recurved 140

140a(139) Axillary leaves not conspicuously auriculate or ciliate, but sometimes peltate . 141
140b Axillary leaves conspicuously auriculate or ciliate, or both 153

141a(140) Lateral leaves tapering from base to apex, with a conspicuous auricle on lower margin . . . . 114. **kunzeana** (p. 312)
141b Lateral leaves parallel-sided or broadest in the middle, without a conspicuous lower auricle, sometimes truncate at base, or with an auricle on the upper side only 142

142a(141) Median leaves with two equally long auricles, the outer broad and the inner narrow 143
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143a(142) Median leaves acute . . . . 115. **lingulata** (p. 312)
143b Median leaves long-aristate . . . . 117. **valida** (p. 313)

144a(142) Median leaves acute 145
144b Median leaves acuminate, cuspidate or aristate 148

145a(144) Median leaves membranous . . . . 118. **calceolata** (p. 314)
145b Median leaves chartaceus 146

146a(145) Median leaves peltate or with two long broad auricles; stems with one stele 119. **marginata** (p. 314)
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147a(146) Lateral leaves 1·5–2·0 (−3) mm; median leaves with two auricles 120. **atirrensis** (p. 317)
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148b Ultimate segments of branch system equally dichotomous, flabellately arranged; axillary leaves not elliptic 151

149a(148) Median leaves aristate, distinctly coarsely toothed; lateral leaves ovate-elliptic, toothed on the acroscopic margin . . . . . . 122. **asplundii** (p. 317)
149b Median leaves acuminate or cuspidate, entire to denticulate; lateral leaves oblong-elliptic, entire to denticulate 150

150a(149) Median leaves acuminate with equal auricles; base of lateral leaves cordate 123. **epirrhizos** (p. 318)
150b Median leaves long-acuminate or cuspidate with unequal auricles; base of lateral leaves with narrow ciliate auricle on acroscopic side . 124. **poeppigiana** (p. 318)

151a(148) Lateral leaves symmetrical and oblong in outline with rounded or very obtuse apex; axillary leaves narrowly oblanceolate . . . 126. **silvestris** (p. 319)
151b Lateral leaves asymmetrical in outline, broadest nearer the base, with pointed apex; axillary leaves ovate or lanceolate 152

152a(151) Lateral leaves distinctly toothed at least on acroscopic margin, ± symmetrical, midrib ± median; median leaves unbordered . . . 127. **trisulcata** (p. 320)
152b Lateral leaves indistinctly toothed, distinctly asymmetrical, midrib closer to posterior margin; median leaves with white borders . . . 125. **suavis** (p. 319)

153a(140) Main stems flagelliform at apex . . . . 129. **sulcata** (p. 321)
153b Main stems not flagelliform at apex 154

154a(153) Stems up to 15 mm across (including leaves), dichotomously branched and flabellate at apex; axillary leaves with two incurved entire auricles; median leaves often paler than lateral leaves 155
154b Stems up to 8(–12) mm across (including leaves), unequally dichotomous or

pinnately branched; axillary leaves with straight or curved dentate to ciliate auricles; median leaves same colour as lateral leaves 156

155a(154) Lateral leaves with two auricles . . . . 128. **sericea** (p. 321)
155b Lateral leaves with one auricle . . . . 116. **articulata** (p. 313)

156a(154) Lateral leaves narrowly oblong; median leaves aristate with one peltate auricle 157
156b Lateral leaves elliptic, elliptic-lanceolate or deltate-ovate; median leaves acute or acuminate, usually with two auricles (the inner one sometimes rudimentary) 160

157a(156) Axillary leaves with long straight subparallel auricles curved at the tips 129. **sulcata** (p. 321)
157b Axillary leaves with short usually wholly curved auricles 158

158a(157) Auricles on upper side of lateral leaves longer than those on the lower side, with cilia 1-celled . . . . 130. **horizontalis** (p. 322)
158b Auricles of lateral leaves subequal, with cilia one or several-celled 159

159a(158) Lateral leaves obtuse, distant, 3–4 leaf-breadths apart on main stem 131. **microtus** (p. 323)
159b Lateral leaves subacute, close, 1–2 leaf-breadths apart on main stem 132. **humboldtiana** (p. 323)

160a(156) Lateral leaves *c.*1·5 mm, lacking posterior auricle . . . . 120. **atirrensis** (p. 317)
160b Lateral leaves (2–) 3·5–5 mm, with ± triangular posterior auricle (often appressed to dorsal side of stem) . . . . 133. **diffusa** (p. 323)

Species

Subgenus SELAGINELLA

1. Selaginella sellowii Hieron. in *Hedwigia* **39** : 306 (1900); Tryon in *Ann. Mo. bot. Gdn* **42** : 34 (1955). Type from Brazil, Praia de San Diego, anno 1821, *Sellow* (B, fragment; NY).
Selaginella rupestris f. *brasiliensis* Milde, *Fil. Eur. Atlant.* : 263 (1867), p.p. Type as above.
Selaginella rupestris f. *amazonica* Milde, *Fil. Eur. Atlant.* : 263 (1867). Type from Peru.
Selaginella rupestris sensu Sodiro, *Crypt. Vasc. Quit.* : 592 (1893), non (L.) Spring (1838).
Selaginella amazonica (Milde) Hieron. in *Hedwigia* **39** : 310 (1900), non *S. amazonica* Spring (1840). Type from Peru.
Selaginella mildei Hieron. in Engl. & Prantl, *Nat. Pflanzenf.* **1** (4) : 671 (1902). Type from Peru.

Specimens seen:
VENEZUELA. Lara: near Barquisimeto, 500 m, *Alston* 6382 (BM).
COLOMBIA. Nariño: Patia Valley, 700—1200 m, *Lehmann* KK97 (K US); Rio Guaitara, Pasto, 1500 m, *Lehmann* BT776 (K, US).
ECUADOR. Without exact locality: *Sodiro* s.n. (B, NY); Valle del Juanambu, *André* 2891 (NY); Quitonian Andes. *Jameson* 12 & 13 (BM); 'Valleys of the Andes', 1800–2100 m, *Jameson* 426 (BM, US). Imbabura: between Chota and Ambuqui, *Fagerling & Wibom* 1333 (S). Pichincha: near Perucho, 1700 m. *Asplund* 20307 (S).
PERU. Amazonas/Loreto: banks of Rio Maranon, near Tomependa, *Bonpland* s.n. (B, holotype; BM, isotype of *S. rupestris* f. *amazonica* Milde). Cajamarca: Jaen, Penco, *Raimondi* 652 (BM).
BOLIVIA. Cochabamba: Cochabamba, 2600 m, *Tutin* 1607 (BM); Cerveceria Colon, 2700 m, *Balls* B. 6229 (US); gravelly, sparsely shrub-covered slope, 2520 m, 3 miles W Quillacello-Cochabamba, *Hermann* 24595 (BM). La Paz: Neuvo mundo, *Troll* 898 (B); Muru Muntani, Larecaja, 1200 m, *Williams* 1400 (NY, US). Santa Cruz: Resinas del Fuerte, Samaipata, 2000 m, *Steinbach* 8254 (NY). Tarija: Toldos, 3200 m, *Fiebrig* 3322 (BM).
BRAZIL. Without exact locality: type as above. Bahia: near Machado Portello, *Rose & Russell* 19937 (NY). Rio de Janeiro: Corcovado, *v. Lützelburg* 18870 (NY); *Lindman*, A 213 (BM); Nictheroy Frubuky, *Brade* 12825 (BM); above garden of British Embassy, Rio Cosme valles 95, *Lutz* 1883 (BM).

Rio Grande do Sul: Santa Angelo, *Jurgens* L 30 (BM); Böhmeback, *Jurgens* L 29 (BM, NY); Montenegro, *Dutra* 1370 (BM).

Geographical range: Cuba and Mexico to Argentina.

Notes: Schomburgk (*Reisen Brit. Guiana* **3** : 794, 880 (1948)) reports *S. rupestris* from British Guiana: 'An den Ufern des Demerara auf lichten Waldstellen'. No one has found any species of this group in the Guianas since, but the record may refer to *S. sellowii* or *S. sartorii.*

2. Selaginella sartorii Hieron. in *Hedwigia* **39** : 304 (1900); Knox in *Trans. bot. Soc. Edinb.* **35** : 245 (1950); Tryon in *Ann. Mo. bot. Gdn* **42** : 36 (1955). Type from Mexico, *Sartorius* s.n. (B).

Seleginella rupestris f. *brasiliensis* Milde, *Fil. Eur. Atlant.* : 263 (1867), p.p. Type from Venezuela.

Seleginella sartorii var. *venezuelensis* Hieron. in *Hedwigia* **39** : 305 (1900). Type from Venezuela.

Seleginella rupestris sensu Kunth in *Reprium Spec. nov. Reg. Veg.* **43** : 94 (1926), non. (L.) Spring.

Specimens seen:
VENEZUELA, Merida: Langunillas, *Marcuzzi* s.n. (BM); near Ejido, 1700 m, *Alston* 6774 (BM); Páramo de Mucuti, Mucuchies, *Moritz* 370 (BM, K, isotypes of *S. sartorii* var. *venezuelensis* Hieron.). Tachira: near la Grita, 1100 m, *Alston* 7051 (BM). Trujillo: between Valera and Timotes, 1800 m, *Alston* 6507 (BM), 6513 (BM).
COLOMBIA. Cundinamarca: Soacha, 2600 m, *Lindig* 1523 (BM). Norte de Santander: Páramo de Fontibon, Pamplona, 2500 m, *Alston* 7285a (BM). Santander: Malaga, 2200 m, *Alston* 7390 (BM).
BOLIVIA. La Paz: Sorata, 2400 m, *Rusby* 462a (NY).

Geographical range: Mexico to Colombia, possibly to Bolivia.

Note: The specimen from Bolivia (*Rusby* 462a) probably belongs here, and we would like to see more material from this area.

3. Selaginella peruviana (Milde) Hieron. in *Hedwigia* **39** : 307 (1900); Knox in *Trans. bot. Soc. Edinb.* **35** : 244 (1950); Tryon in *Ann. Mo. bot. Gdn* **42** : 77 (1955). Type from Peru, Huanuco, *Ruiz* s.n. (NY).

Selaginella rupestris f. *peruviana* Milde, *Fil. Eur. Atlant.* : 263 (1867). Type as above.

Lycopodioides rupestris sensu Kuntze, *Rev. Gen.* **3** : 379 (1891), non (L.) Kuntze.

Specimens seen:
ECUADOR. Without precise location: Nabón, *Rose* 23039 (NY). Loja: bank of Rio Arenal, Puente Buquerón, SW of Catamayo, *Asplund* 18064 (S).
PERU. Without precise locality, *Diehl* 2517 (BM), 2565 (BM). Cuzco: Urubamba Valley, 150 m, *Tutin* 1359 (BM). Huanuco: type as above. Junin: Orora, *Rose* 19468 (NY). Lima: Matucana, 2400 m, *Wilkes* s.n. (NY); 2400 m, *Asplund* 11093 (S).
BOLIVIA. Without precise locality: *Bang* 111 (NY); *Kuntze* s.n. (NY). La Paz: Sorata, *Mandon* 1531 (BM); vicinity La Paz, 3000–3450 m, *Cardenas* 46 (NY); *Rose* 18845 (NY); *Williams* 2649 (NY); *Bang* 120 (NY); Obrajas near La Paz, 3300 m, *Buchtien* 4299 (NY); Talca Chugiaguillo, *Bang* 787 p.p. (NY).

Geographical range: Oklahoma and New Mexico, south to Argentina.

Subgenus STACHYGYNANDRUM

4. Selaginella convoluta (Arnott) Spring in Martius, *Fl. Bras.* **1** (2) : 131 (1840), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 69 (1850); R. Schomburgk, *Reise, Brit. Guiana* **3** : 880 (1848); Baker, *Fern Allies* : 88 (1887); Maury in *J. Bot., Paris* **3** : 130 (1889). Type from Brazil, Rio de Janeiro, *Jameson* s.n. (E).

Lycopodium convolutum Arnott in *Mem. Wernerian nat. Hist. Soc.* **5** : 199 (1824); reimpr. in *Mém. Soc. Hist. nat. Paris* **1** (2) : 327 (1824). Type as above.

Lycopodium convolutum (Beauv.) Desv. (1814), nom. illeg. [published only in synonymy].

Lycopodium bryopteris sensu Aublet, *Hist. Pl. Guiane Franç.* **2** : 967 (1775), non L.

Lycopodium hygrometricum Martius, *Reise in Bras.* **2** : 792 (1828). Type from Brazil.

Lycopodium revolutum Hook & Grev. in Hook., *Bot. Misc.* **2** : 381 ['281'] (1831).

Selaginella hygrometrica (Martius) Spring ex Martius in *Flora, Jena* (Beibl.) **1837** (2) : 126 (1837). Type as above.

Selaginella orbignyana Spring ex Decaisne, *Arch. Mus.* **2** : 194 (1841–42), nom. nud.; in *Bull. Acad. r. Belg.* **10** : 136 (1843); in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 68 (1850). Type from Bolivia.

Selaginella longispicata Underw. in *Publs Field Mus.* (Bot.) **1** : 287 (1896); Hieron. in *Hedwigia* **63** : 286 (1917). Type from Mexico.

Specimens seen:
GUYANA. Demerara: without further locality, *Hancock* s.n. (K).
VENEZUELA. Without precise locality: *Stevens* s.n. (NY). Lara: near Barquisimeto, 500 m, *Alston* 6383 (BM).
COLOMBIA. Magdalena: Santa Marta, *Purdie* s.n. (BM); Valle Dupar, *Haught* 2338 (BM, COL); San Sebastian, Sierra Nevada de Santa Marta, 6200 m, *Foster & Smith* 1512 (COL).
BOLIVIA. Santa Cruz: Yuanatos, Prov. Chiquitos, *D'Orbigny* 263 (P, type of *S. orbignyana*).
BRAZIL. Without exact locality: *Redondo* s.n. (BM); *Glaziou* 1217 (C). Bahia: near Machado Portello, *Rose & Russell* 20012 (NY); Barlima, *Rose & Russell* 19796 (NY); Caetano-Nazareth, Pernambuco, *Werdermann* 2826 (B). Minas Gerais: near Juiz de Fora, *Damazio* 727 (P). Paraiba: Serra d'Olho D'Agua, Buquarao, *Luetzelburg* 287 (M). Piaui: Catingas Sertao, *Gardner* 2020 (BM). Rio de Janeiro: *Regnell* 368 (C); *Glaziou* s.n. (C); Serra Estrella, Frade, *Luetzelburg* 272 (B, M); Leme, *Luetzelburg* 52 (M). São Paulo: *Usteri* 26a (P); Salto Grande do Paranapanema, *Edwall* 4950 (S).

Geographical range: Guatemala and Greater Antilles through to Paraguay. Quoted by Aublet (1775) as being in French Guiana and by Schomburgk (1848) as in the Canuku Mountains.

5. Selaginella pallescens (C. Presl) Spring in Martius, *Fl. Bras.* **1** (2) : 132 (1840); Alston in *J. Bot., Lond.* **72** : 226 (1934), *Bull. Br. Mus. nat. Hist.* (Bot.) **1** (8) : 231 (1955). Type from Mexico, *Haenke* s.n. (PR).

Lycopodium pallescens C. Presl, *Rel. Haenk.* **1** : 79 (1825). Type as above.

Lycopodium cuspidatum Link, *Hort. Reg. Bot. Berol.* **2** : 161 (1833). Type from Mexico.

Selaginella cuspidata (Link) Link, *Fil. Spec. in Hort. Reg. Bot. Berol. Cult.* : 158 (1841). Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 66 (1850); Baker, *Fern Allies* 89 (1887); Hieron. in *Hedwigia* **58** : 286 (1917). Type as above.

Selaginella sulcangula Spring in *Bull. Acad. r. Belg.* **10** : 137 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 163 (1850), p.p. excl. planta jamaicensis. Type presumably from Venezuela. [Not collected by Plée in Colombia as stated by Spring.]

Selaginella cordata Klotzsch in *Linnaea* **18** : 524 (1844), nom. superfl. (cites *L. cordifolium* Desv.) p.p. quoad spec. *Moritz* 67.

? *Selaginella cordifolia* sensu Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 103 (1850), p.p. quoad *Moritz* 67.

Selaginella emmeliana van Geert in *Rev. Hort. Belg. Étrang.* **10** : 220 (1884). Type from 'Quinquina, South America'.

Specimens seen:
VENEZUELA. Without precise locality: *Funck & Schlim* 331 (BM). Aragua: below Guarnitas, Parque Nacional, 700 m, *Alston* 5859 (BM); Colonia Tovar, *Moritz* s.n. (NY); *Fendler* 321 (NY). Federal District: Venta Grande de Caracas, *Moritz* s.n. (NY); between Cotiza and los Venados, *Allart* 29 (NY, VEN); Between La Guayra and Caracas, *Kuntze* s.n. (NY); Silla de Caracas, *Kuntze* s.n. (NY); Cerro de El Avila, 1600 m, *Pittier* 29 (NY); Los Flores, Cerro de El Avila, 1600 m, *Alston* 5535 (BM); Galipan, *Moritz* 71 p.p. & 221 p.p. (BM); near Caracas, *Ernst* 212 (BM). Merida: Merida, *Moritz* 315 & 316 (BM).

Miranda: Sebucan near Dos Caminos, *Pittier* 11918 (NY, VEN); Las Mostazas, between los Teques and Tejerias, 963 m, *Allart* 184 (VEN).
Monagas: Cerro de la Cuevade Dona Anita, *Steyermark* 61881 (BM); Caripe, *Moritz* 68 (BM).
COLOMBIA. Without precise locality: *Moritz* 69 (BM), 382 (BM). Magdalena: Santa Marta, *Purdie* s.n. (BM); near Santa Marta, *Baker* 6 (NY); Onaca Road, Santa Marta, 360 m, *Smith* 2243 (BM, NY, US); 7 ml E of Bonda, 600 m, *Smith* 2470 (NY). Valle del Cauca: Cartago, 1950 m, *Kuntze* s.n. (NY).

Geographical range: Mexico to Colombia. Alston (1936) records a specimen of this species from Brazil (Santa Catarina: Joinville, *Schmalz* 148 (NY)) which is now believed to be an escape from cultivation.

Notes: It is not clear as to how Moritz collections became so mixed under especially nos 71 and 221 (see page 272).

6. Selaginella erythropus (Martius) Spring in Martius, *Fl. Bras.* **1** (2) : 125 (1840), in *Bull. Acad. r. Belg.* **10** : 225 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 155 (1850), excl. var. *major*; Baker, *Fern Allies* : 103 (1887), excl. var. *major*; Knox in *Trans. bot. Soc. Edinb.* **35** : 282 (1950). Type from Brazil : Piaui, *Martius* s.n. (BR, not seen).

Lycopodium erythropus Martius, *Icon. Select. Pl. Crypt. Bras.* 39 (1834). Type as above.

Selaginella setosa Linden, *Cat.* **23** : 9 (1869), *Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten* **12** : 189 (1869). Type from Colombia.

Selaginella erythropus var. *minor* Will. Watson in *Gdnrs' Chron.* III, **14** : 651 (1893) nom. nud.; Hieron. in *Hedwigia* **58** : 288 (1917). Type from 'Andes.'

Selaginella pitcheriana Will. Watson in *Gdnrs' Chron.* III, **14** : 651 (1893), nom. nud. in synonymy.

Specimens seen:
COLOMBIA. Caldas: Santa Cecilia, Pueblo Rico, 800 m, *v. Sneidern* 5053 (S). Cundinamarca: Tocarina, *Lindig* 1510 (BM). Tolima: Pièdras, *André* s.n. (NY); R Saldana, 400 m, *Haught* 6379 (BM); Valle del Cauca: Chuchilla E. of Zarzal, 11–1300 m, *Pennell, Killip & Hazen* 8504 (NY, US).
ECUADOR. Guayas: Cerro de Soulana, Guayaquil, *Jameson* 585 (BM, US); Puna Is., *Barclay* 662 (BM); Guayaquil, *Fraser* s.n. (BM). Manabi: Salanga, *Barclay* 652 (BM); *Pinchincha:* S Jose de Toachi, W of Quito, 915 m, *Bell* 194 (BM).
PERU. Ayacucho: Estrella, between Huanata and Rio Apurimac, 500 m, *Killip & Smith* 22664 (BM, NY). Junin: Colonia Perene, 600 m, *Killip & Smith* 24918 (BM, NY). Loreto: near Tarapato, *Spruce* 3989 (BM, NY, US). San Martin: Juan Jui, Alto Rio Huallaga, 4–800 m, *Klug* 4267 (BM, COL); S bank of Perene River, within 15 m of confluence of Chanchamayo and Paucartambo, 670 m, *Gascoyne-Cecil* 6a (BM), 82a (BM); La Merced, *Killip & Smith* 23802 (BM, NY); Schunke Hacienda, above San Ramon, 1300–1700 m, *Schunke* A 247 (BM); Chanchamayo Valley, *Schunke* 190 (BM).
BOLIVIA. Beni: Sécure, Guanay to Carahuarani, 548–914 m, *Tate* 1213 (US); Campolican, Rurrenabaque, *Rusby* 764 (NY, US). La Plaz: San Buena Ventura, *Williams* 1399 (NY, US); Yungas, Rio Bopi Valley, *Rusby* 337 (NY, US).
BRAZIL. Without exact locality: *Glaziou* 13364 (BM, C). Bahia: Fazend Barauna, 5 km S of Barreiras, *Black* 17877 (BM, IAN). Ceara: *Bolland* s.n. (K). Matto Grosso: Palmerras, *Lindman* A 2589 (BM). Minas Gerais: Near Diamantina, *Moore* 499 (BM); Macahuba, *Silveira* 394 (BM); between Sta Luzia do Rio das Velhas e Macaubas, *Damazio* 27384 (P); Lagoa Santa, *Glaziou* 22645 (G); Serra do Cipó, *Damazio* 1999 (BM). Piaui: without further locality, *Gardner* 2386 (M, P). Rio de Janeiro: *St. Hilaire* 162 (P); *Hoehne* 921 (BM).

Geographical range: Colombia to Bolivia and east to the states of Piaui and Ceará in Brazil.

7. Selaginella umbrosa Lemaire ex Hieron. in Engl. & Prantl, *Nat. Pflanzenf.* **1** (4) : 683 (1901); in *Hedwigia* **58** : 287 (1917); Knox in *Trans. bot. Soc. Edinb.* **35** : 276 (1950); Alston in *Bull. Br. Mus. nat. Hist.* (Bot.) **1** : 30 (1952). Type from (?) Guatemala.

Lycopodium umbrosum Lemaire ex Kuntze in *Linnaea* **23** : 292 (1850), nom. nud., in syn., non Bory ex Willd. (1810). Type as above.

Selaginella erythropus var. *major* Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 156 (1850); Baker, *Fern Allies* : 103 (1887). Type from Guatemala.

Selaginella lemairei Hieron. in *Hedwigia* **58** : 287 (1917), nom. provis.

Specimens seen:
COLOMBIA. Antioquia: Turbo, *Schott* 1 (NY); *Haught* 4800 (BM).

Geographical range: Yucatan to Colombia; also in Tobago, where possibly introduced.

8. Selanginella haematodes (Kunze) Spring in Martius, *Fl. Brasil.* **1** (2) : 126 (1840), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 156 (1850); Baker, *Fern Allies* : 103 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 274 (1950); Alston in *Bull. Br. Mus. nat. Hist.* (Bot.) **1** : 234 (1955). Type from Peru, Loreto: Tocache Mission, *Poeppig* s.n. (K).

Lycopodium haematodes Kunze in *Linnaea* **9** : 9 (1835), *Farrnkr.* **2** : 61 [excl. t.30 fig. C] (1843). Type as above.

Selaginella filicina Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 189 (1850). Syntypes from Venezuela and Peru.

Selaginella rosea Alston in *J. Bot., Lond.* **70** : 281 (1932). Type from Colombia.

Specimens seen:
VENEZUELA. Carabobo: San Esteban, near Puerto Cabello, 200 m, *Alston* 6109 (BM); *Pittier* 9234 (NY, VEN). Federal District: Hacienda El Limón, valley of Puerto La Cruz, 500–1000 m, *Pittier* 9234 (NY, VEN).

COLOMBIA. Without precise locality, *Triana* s.n. (NY). Antioquia: Santa Elena, *Archer* 1185 (BM, US); Ocateado, 2300–2600 m, *Kalbreyer* 1941 (K); El Penol, *Daniel* s.n. (BM); Las Isletas, *André* 434 (NY); Villa Artega 3750–5000 m, *Gutierrez & Barkley* 17c108 (BM, S). Cauca: Rio Huangubio, near Popayan, 1700–1800 m, *Lehmann* B T 875 (K, holotype of *S. rosea* Alston; NY, US). Chocó: Truando Falls, *Schott* 7 (NY). Cundinamarca: near Bogota, *Joseph* A 465 (US); 1000 m, *Triana* s.n. (NY); Quebrada de Susumuco, *André* 963 (NY); Susumuco, 1000 m, *Triana* 696 (BM); La Palma, *Triana* s.n. (BM); Tequendama Falls, *Joseph* A 914 (BM); Paime, *Joseph* 1084 (BM). Meta: Villavicencio, *Perez Arbelaez* 7 (BM, US); 5000 m, *Alston* 7469 (BM); Rio Negro, S of Villavicencio, 457 m, *Wright-Barker* s.n. (BM); Plaza Bonita, Sierra Macarena, *Philipson, Idrobo & Fernandez* 1415 (BM); Sierra La Macarena, between Guapayita and 'Caño 20', *Idrobo* 4772 (BM). Nariño: Putamayo upstream from Puerto Asis, *Barclay* 4754 (COL); Cordillera Oriental, Oreto, on Rio Oretopunqo, *c.* 450 m, *Ewan* 16769 (BM). Santander: between Lebrija and San Vicente, 1400 m, *Alston* 7346 (BM).

ECUADOR. Napo-Pastaza: Tena, *Asplund* 10188 (S); Mera, *Asplund* 18790 (S); between Puyo and Candos, 325–375 m, *Mexia* 6843 (BM); Tnte. H. Ortiz, 18 km from Puya on road to Tena, approx. 1 km E of the road, 1100 m, *Øllgaard & Balsley* 9232 (AAU). Santiago-Zamora: near Zamora, E of Loja, *Camp* E 50 (BM); between Rio Sabanilla and Canillones Tambo, 1370–2133 m, E of Loja, *Camp* E 64 (BM).

PERU. Loreto: type as above; Tarapoto, *Spruce* 4036 (BM, NY); Puerto Arturo, 135 m, *Killip & Smith* 27747 (BM, NY); Lower R Huallaga, *Williams* 5359 (BM); Huanuco: near Riachuelo Chontalagua, *Mexia* 8302 (BM); Near Tingo Maria, *Asplund* 12072 (S), 12198 (S); 500–600 m, *Ferreyra* 1591 (BM), 2891 (BM), 2191 (BM); junction of Rio Monzón and Rio Huallaga, *Asplund* 12693 (S). Junin: Rio Paucartambo Valley, near Perene Bridge, 700 m *Killip & Smith* 25292 (BM, NY); Cahupanas on Rio Pichis, 340 m, *Killip & Smith* 26776 (BM, NY); between Meriatiriani and Puero Yessup, *Killip & Smith* 26214 (BM, NY); Ucayali, *Huber* 1430 (BM); Perene River, within 15 m of confluence of Chanchaymayo and Paucartambo Rivers, 1219 m, *Gascoyne-Cecil* 44 (BM). San Martin: Alto Rio Huallaga, *Williams* 6780 (BM).

BOLIVIA. Without precise locality: *Kelly* s.n. (BM). Beni: Mapiri, 487 m, *Williams* 1397 (NY); 1524 m, *Rusby* 450 (NY); Rio Chimate, 579 m, *Tate* 515 (BM); Charopampa near Mapiri, 570 m, *Buchtien* 623 (NY); San Antonio near Mapiri, *Buchtien* s.n. (Rosenst. exsicc. 94; BM). Chapare: Rio Juntas, *Kuntze* s.n. (NY). Cochamba: Espirito Santo, near Cochamba, *Bang* 1286 (BM, NY). La Paz: Polo-Polo near Coroico, prov. Yungas, 1100 m, *Buchtien* 624 (NY); Hacienda Sinaco, on way to Tipuani, 1400 m, Larecaja, *Buchtien* 5275 (BM); Bopi River Valley, Yungas mnts, 762 m, *White* 449 (NY); 914 m, *Rusby* 335 (NY), 377a (NY), 710 (NY); Tumapaca, *Cardenas* 1974 (NY).

Geographical range: Panama southwards to Bolivia.

Notes: Alston (1932) described *S. rosea* from Colombia. We can see no difference between those specimens and pale forms of typical *S. haematodes.*

9. Selaginella coarctata Spring in Martius, *Fl. Bras.* **1** (2) : 126 (1840), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 164 (1850); Baker, *Fern Allies*: 101 (1887). Type from Brazil, Amazonas: Arara-Coara Mts, Rio Japura, *Martius* s.n. (M, fragment; BM).

Selaginella puberula Klotzsch in *Linnaea* **18** : 522 (1844); Schomb., *Reise. Brit. Guiana* **3** : 1042 (1848); Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 165 (1850); Baker, *Fern Allies* : 101 (1887), p.p. excl. pl. peruviana; Knox in *Trans. bot. Soc. Edinb.* **35** : 254 (1950). Type from Brazil.

Specimens seen:
COLOMBIA. Vaupés: Raudal de Yurupari, Rio Vaupés, *Schultes & Cabrera* 19742 (US), 19748 (US); Cano del Caribe, Rio Guainia, 250–280 m, *Schultes, Baker & Cabrera* 18265 (US).
BRAZIL. Amazonas: type as above; Rio Padauiri, *Schomburgk* 979 (BM, K, US); Campo on Rio Padauiri, *Traill* 1417 (K).

Geographical range: Eastern Colombia to north-west Brazil. Alston (1936) states 'British Guiana', assuming Schomburgk collected it on the nort-east side of Mt Roraima. In fact this reference to Roraima itself must be considered very doubtful, as the Schomburgk specimen (979) in K is labelled 'Rio Padauiri' and his manuscript catalogue adds: 'grows in sandy savannahs'. It has never been recollected on Roraima; but Traill did get it again on the Rio Padauiri, and this is also the locality mentioned by J. Smith in *J. Bot., Lond.* **1** : 203 (1842).

Notes: This species superficially resembles *Selaginella asperula* (No. 107), but the stems are pubescent, ex-articulate and terete (not glabrous, articulate and usually quadrangular), while the microspores have a plane (not convoluted) wing and larger warts. The pubescent branches separate *S. coarctata* from all other American species, except *S. exaltata* (No. 104). *S. puberula* Klotzsch is based on a more luxuriant specimen, and is within the range of variation of *S. coarctata.*

10. Selaginella longissima Baker in *J. Bot., Lond.* **19** : 208 (1881), **21** : 334 (1883), *Fern Allies* : 60 (1887); Hieron. in *Bot. Jb.* **34** : 580 (1905); Knox in *Trans. bot. Soc. Edinb.* **35** : 289 (1950). Type from Colombia, Antioquia: Murri, 915 m, *Kalbreyer* 1815 (K).

Specimens seen:
COLOMBIA. Antioquia: type as above. Cauca: Island of Gorgona, *Cheesman* 2a (BM). Chocó: Alto de Buey, Nuqui, *v. Sneidern* A. 10 (S); Rio Nuqui, 200 m, *Haught* 5466 (BM, COL); between La Oveja and Quibdó, *Archer* 1743 (BM); La Concepción, 15 km E of Quibdó, *Archer* 1964 (US); 1999 (US); Quibdó, Rio Atrato, 60 m, *Archer* 2025 (US). Narino: near Altoquer, 1000 m, *Lehmann* 85 (BM); Barbacoas, *Alston* 8520 (BM). Valle del Cauca: near Buenaventura, *Alston* 8663 (BM); *Killip* 11751 (US), 11756 (US); Sabaletas, 25 m, *Killip & Cuatrecasas* 38786 (BM); near Cordova, Rio Dagua, 80–100 m, *Lehmann* 1868 (BM); *Pittier* 525 (BM); *Killip* 5044 (NY, US), 5091 (BM, NY), 5253 (NY, US), 11781 (NY, US), 12154 (US).

Geographical range: confined to Colombia and to lower elevations.

Notes: In *Killip* 12154 the costae of the leaves are thickened and blackened, perhaps because of a fungus disease. Similar states are known in other species, for example, *S. novae-hollandiae* (No. 45) and *S. muscosa* (No. 88).

11. Selaginella mazaruniensis ['mazaruniense'] Jenman in *Gdnrs' Chron.* **22** : 210 (1897), *Ferns Brit. W. Indies* : 404 (1909). Type from Guyana, Essequibo: Mazaruni River, *Jenman* s.n. (NY, holotype; BM, isotype).

Selaginella anceps sensu Wright in *Trans. Linn. Soc. Lond.* **6** : 88 (1901), non *Lycopodium anceps* C. Presl (1825).

Specimens seen:
GUYANA. Essequibo: type as above; Potaro River, *im Thurn* 78 (K); Amatok, Potaro R, *Jenman* s.n. (BM, K, NY); *Sandwith* 1248 (BM, K); foot of the Kaieteur Falls, Potaro R, *Jenman* 1478 (K), s.n. (NY); *Maguire & Fanshawe* 23024 (BM), 23025 (BM); Macreba Falls, Kurufing R, *Altson* 342 (K); Mazaruni R, *Jenman* 7221 (K); Kaieteur Falls, *Appun* s.n. (BM); *Tutin* 518 (BM); Essequibo R, *Jenman* s.n. (BM); Roraima Range, 1066 m, *McConnel & Quelch* 706 (BM, K).

Geographical range: Confined to the sandstone area of Guyana.

12. Selaginella palmiformis Alston ex Crabbe & Jermy in *Am. Fern. J.* **63** : 141 (1973). Type from Venezuela, Amazonas: near Salte de Huá, in western foothills of Serra Imeri, 800 m, *Holt & Blake* 490 (US, holotype; BM, isotype).

Specimens seen:
VENEZUELA. Amazonas: type as above; slopes of Mt Duida, 227 m, *Tate* 376 (NY).
COLOMBIA. Amazonas: Rió Miritiparaná 212 m, *Schultes & Cabrera* 16471 (BM, US). Vaupés: Cerro Isibukuri, Rio Kananari, 250–700 m, *Schultes & Cabrera* 14465 (US); Río Guainia, Río Naquieni, vicinity of Cerro Monachi, *Schultes & Lopez* 10104 (BM); Caño Teemeeña, Rio Piriparaná (tributary of R Apaporis), *Schultes & Cabrera* 17190 (COL, US), 17369 (COL, US), 17396 (US); Caño Oe-gë -dja, Jinogejé, Río Apaporis, *Schultes & Cabrera* 17058 (BM, US).

Geographical range: Confined to the Sierras of the Amazonian part of Venezuela and Colombia.

13. Selaginella flabellata (L.) Spring in *Flora, Jena* **21** : 198 (1838), *Bull. Acad. r. Belg.* **10** : 225 (1843); Baker, *Fern Allies* : 98 (1887); Alston in *Bull. Br. Mus. nat. Hist.* (Bot.) **1** : 31 (1952).
var. **latifrons** A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 278 (1865). Type from Venezuela, Mérida: Colonia Továr, *Fendler* 493 (BM).
Selaginella mortoniana Alston MS, non Crabbe & Jermy.

Specimens seen:
VENEZUELA. Aragua: near El Portachuela, Parque Nacional, 1100 m, *Williams & Alston* 172 (BM, US); Rancho Grande, *Tschudi* 38 (US). Mérida: type, as above.

Geographical range: Confined to the Cordiera Costanera of Venezuela.

Notes: S. flabellata var. *flabellata* is confined to the Lesser Antilles.

14. Selaginella mortoniana Crabbe & Jermy in *Am. Fern J.* **63** : 139 (1973). Type from Colombia, Tolima: near Mariquita, *Linden* 1004 (BM, holotype: BR, K, isotypes).
Selaginella flabellata sensu Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 174 (1850), p.p. quoad pl. *Linden* 1004, non *Lycopodium flabellatum* L. (1753).
Selaginella aciculata Alston MS.
Selaginella hebetata Alston MS.

Specimens seen:
COLOMBIA. Without precise locality: *Linden* 1002 (BM); *Funck & Schlim* 57 (BM). Antioquia: Antioquia, *Kalbreyer* 2037 (BM). Boyacá: Emerald Mines, Muzo, 700 m, *Lindig* 1515 (BM). Cundinamarca: La Vega, 1200 m, *Lindig* s.n. (BM); La Palma, *Lindig* s.n. (BM); Cordillera de Bogota, *Triana* s.n. (BM). Tolima: type, as above.
ECUADOR. Napo: at Rio Payamino, 60 km W of Coca, 350 m, *Holm-Nielsen & Jeppeson* 747 (AAU); at Rio Suno 3 km W of Rio Napo, 400 m, *Holm-Nielsen & Jeppeson* 844 (AAU).

Geographical range: Colombia and north-east Ecuador.

15. Selaginella lechleri Hieron. in Engl. & Prantl, *Nat. Pflanzenf.* **1** (4) : 683 (1901), in *Hedwigia* **41** : 190 (1902). Type from Peru, Puno: near San Gavan, *Lechler* 2159 (BM).

Specimens seen:
COLOMBIA. Amazonas: Cachivera de Jirijirimo, Rio Apaporis, 250 m, *Schultes & Cabrera* 12932 (COL, US), 14048 (COl, US); Soratama, Rio Apaporis, *Schultes & Cabrera* 16080 (US); Caño Peritomé, below Raudal Yayacopi, 227 m, *Schultes & Cabrera* 15526 (US). Vaupés: Caño Teemeena, Rio Piraparaná, *Schultes & Cabrera* 17185 (COL, US); Alto Vaupés, between Plendaiva and Karurú, 400 m, *Garcia-Barriga* 15009 (COL).
PERU. Cuzco: between Mistiana and Keros, 700 m, *Vargas* 7372 (BM), 7393 (BM). Junin: Puerto Bermudez, 375 m, *Killip & Smith* 26467 (BM). Puno: type, as above.

Geographical range: Colombia to south Peru.

16. Selaginella cheiromorpha Alston, **sp. nov.** (Figs 2 & 3)
Species heterophylla ex affinitate *S. quadrifariae* sed foliis caulium minoribus et microsporis laevibus differt.

Planta e basi repente erecta; *caulibus* glabris, usque ad 44 cm altis, basi 3 mm in diam.; parte inferiore simplici 4–23 cm longa, in siccitate straminea; rhizophoris basi restrictis, singulis vel binis; sobolis adeuntibus; parte frondosa ambitu late ovata, ramis usque ad 2·5 cm inter se distantibus, bipinnatis ambitu deltoideis vel ellipticis, usque ad 15 cm longis et 12 cm latis. *Folia caulium* homomorpha distantiaque, oblongo-obovata serrulata, brevissime acuminata, 3 mm longa, 2·5 mm lata; *folia lateralia* horizontaliter patentia, plerumque leviter imbricata oblique ovato-oblonga, *c.* 6 mm longa, 3 mm lata, supra flavoviridia, subtus minus obscura; semifacie superiore semi-ovata, basi cordata, omnino serrata, serrulis partis basalis longioribus; semifacie inferiore semioblonga basin versus integra, apicem versus serrulata et cuneata; *folia axillaria* ovata, basi rotundato-cordata, 4·5 mm longa, 2·5 mm lata, serrata; *folia intermedia* obovato-oblonga, 2·5 mm longa, 2 mm lata, imbricata, fere aequilateralia, sed obliqua, apice acuto, vel brevissime apiculato, ciliolata. *Strobili* in apicibus ramulorum singulatim dispositi, tetragoni, 1 cm longi, 2·25 mm lati, nunquam ramosi; *sporophylla* ovato-deltoidea, carinata, serrata, apice brevissime apiculato; *megasporae c.* 360 μm crassae, subtiliter reticulatae; *microsporae c.* 24 μm crassae, pallide lutescentes, subtiliter granulatae.

Typus: Colombia, Valle del Cauca : ad flumen Dagua, 950 m, *Alston* 7897 (BM, holotype).

Other specimens seen:
COLOMBIA. Valle del Cauca: valley of R. Dagua, 950 m *Alston* 780 IA (BM); 1050 m, *Alston* 7893 (AAU, BM, COL, INPA, USM, US, VEN); La Cumbre, 1800–2100 m, *Pennell* 5901 (NY, US).

Geographical range: Confined to the western cordillera of Colombia.

17. Selaginella terezoana Bautista in *Bolm. Mus. Para. Emilio Goeldi* (Bot.) II, **45** : 1 (1974). Type and sole specimen seen from Brazil, T. F. Roraima, '5°08′N—60°40′W', *Terezo* 32 (IAN).

Geographical range: Only known from the type (above). The label cites coordinates which are in lowland Amazonas but it adds 'Floresta Umbrofilia Sub-tropical,' suggesting montane forest.

Note: The type specimen is sterile, but the very long cilia on the cauline and median leaves are most distinctive and like no other species.

18. Selaginella anceps (C. Presl) C. Presl, in *Abl. Böhm. Ges.* V, **3** : 581 (1844); Alston in *J. Bot., Lond.* **72** : 225 (1938); Knox in *Trans. bot Soc. Edinb.* **35** : 282 (1950). Type probably from Peru, *Haenke* s.n. (PR).

Lycopodium anceps C. Presl, in *Rel. Haenk.* **1** : 80 (1825). Type as above.

Lycopodium gracile Desv. ex Poiret, *Encycl. Meth. Bot.* Suppl. **3** : 551 (1814). Type from Peru.

Selaginella gracilis (Desv.) Hieron. in *Hedwigia* **58** : 292 (1917), non Moore (1886). Type as above.

Selaginella flabellata sensu Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 174 (1850),p.p. pl. peruv. et var. *expansa*: Baker, *Fern Allies* : 98 (1887), p.p. quoad pl. andina, excl. syn. L.

Selaginella casequiarensis Hieron. ex Bonap., *Notes Pterid.* **1** : 179 (1915), nom. nud.

Specimens seen:
VENEZUELA. Bolívar: at the foot of Cerro Imei, Rio Pacimoni, *Spruce* 3380 (BM).
COLOMBIA. Caquetá: Florentia, Quebrada de la Perdices, 400 m, *Cuatrescasas* 8851 (US). Valle del Cauca: Cordoba, 80–100 m, *Killip* 11811 (NY).
ECUADOR. Napo-Pastaza: Tena, *Asplund* 8909 (S).
PERU. Without precise locality or collector: *Herb. Desvaux* (P, type of *L. gracile* Desv.); type, as above. Ayacucho: Estrella between Huanta and Rio Apurimac, 500 m, *Killip & Smith* 22671 (BM, NY).

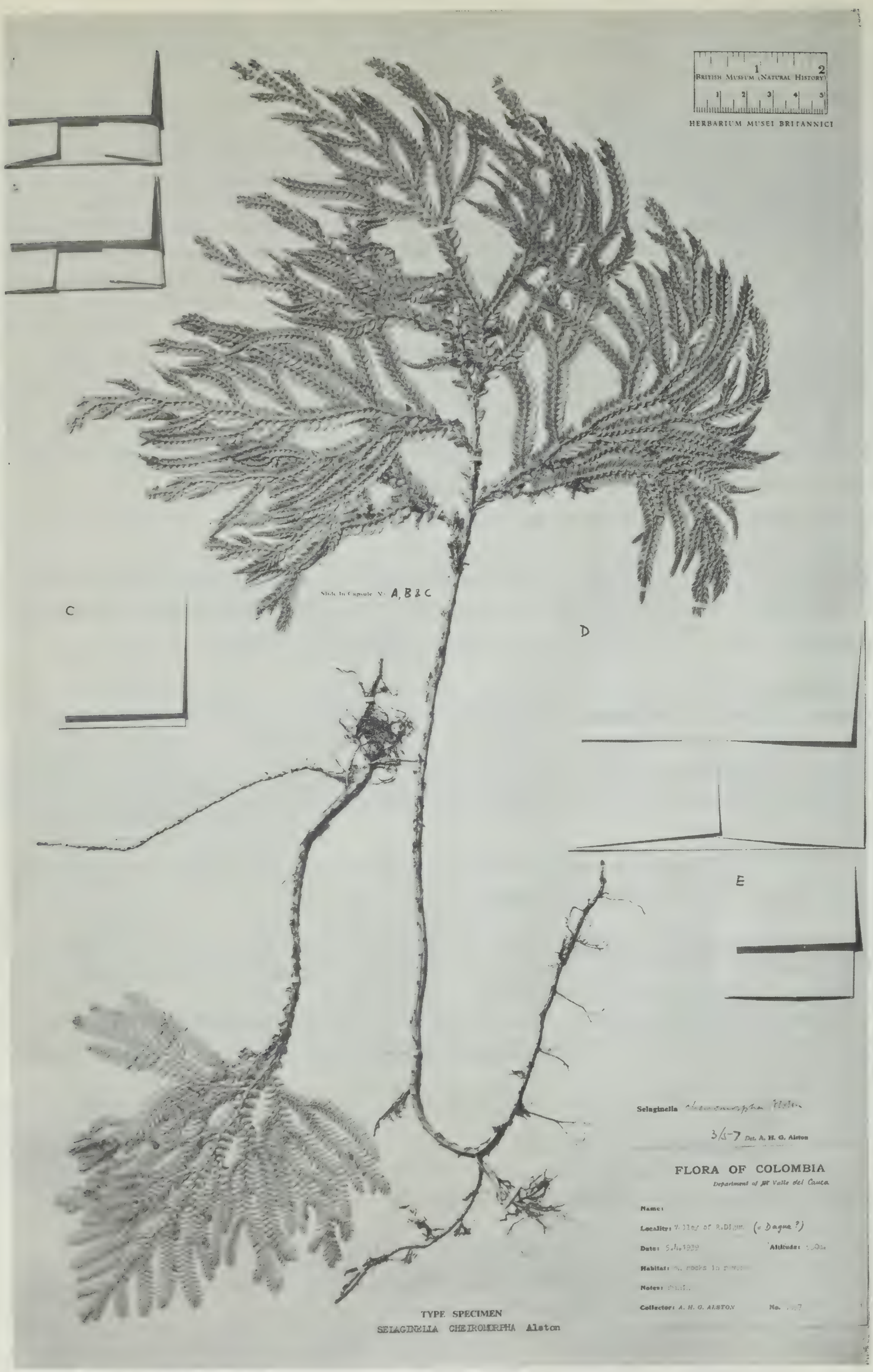

Fig. 2 *Selaginella cheiromorpha* Alston: Type specimen, *Alston* 7897 (BM).

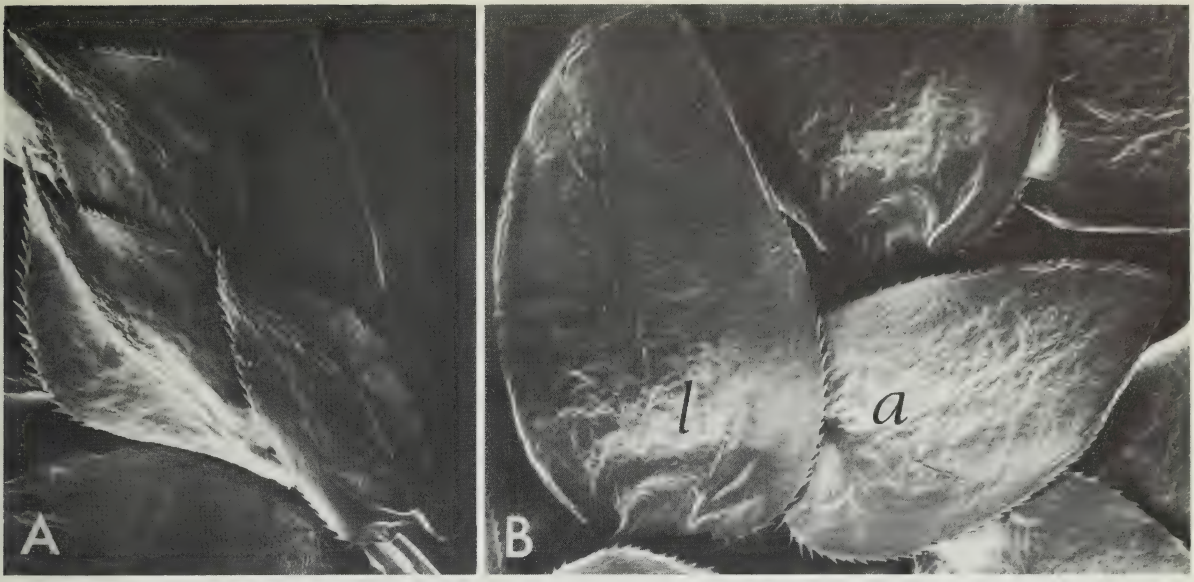

Fig. 3 *Selaginella cheiromorpha* Alston: **A.** Close-up of median leaves, × 16. **B.** Close-up showing lateral (*l*) and axillary (*a*) leaves, × 16. All from *Alston* 7897.

Junin : Rio Pinedo, N of La Merced, 700–900 m, *Killip & Smith* 23605 (BM, NY); Rio Paucartambo Valley, near Perene Bridge, 700 m, *Killip & Smith* 25267 (BM, NY); along Rio Perene, near Colonia Perene, 600 m, *Killip & Smith* 25104 (BM, NY); on south bank of Perene River within 15 m from confluence of Rio Chanchosmayo and Rio Paucartambo, 670 m, *Gascoyne-Cecil* 6 (BM); Chanchosmayo, *Schunke* s.n. (BM, P). Loreto: Tarapoto, *Spruce* 4053 (BM, NY); 750 m, *Williams* 6056 (BM); Creek Inche above Pongo de Manseriche, 215 m, *Mexia* 6371 (BM); Sierra del Pongo, 400 m, *Mexia* 6185 (BM). San Martin: Juan Jui, Alto Rio Huallaga, 400 m, *Klug* 3831 (BM). Huanuco: Cochero, *Dombey* s.n. (BM); Tulmayo, near Tingo Maria, 6–700 m, *Ferreyra* 2161 (BM); near confluence of Rio Cayumba and Huallaga, 795–850 m, *Mexia* 8262 (BM); Pampayaco, *Kanehira* 118 (US).
BOLIVIA. Without precise locality: *Bridges* s.n. (BM); *Kelly* s.n. (BM). La Paz: Isapuri, Laracaja, 500 m, *Williams* 1398 (NY, US).

Geographical range: Costa Rica southwards to Bolivia.

Notes: The stem leaves of this species are almost uniform and directed upwards almost to the apex of the main stem, giving the plant a distinctive appearance. Presl's type in the herbarium of the National Museum at Praha is localized Luzon, but it was probably from Peru. *S. casequiarensis* Hieron. was so labelled on an herbarium sheet, but never validly published. Alston in MS was inclined to validate that taxon at specific rank, citing *Spruce* 3380 (BM) as type. In our view the difference, i.e. the more pronounced cilia on the lateral leaves, is within the range of *S. anceps*.

19. Selaginella hirsuta Alston ex Crabbe & Jermy in *Am. Fern J.* **63** : 138 (1973). Type from Venezuela, Bolivar: southeastern base of Carrao-tepui, 1460–1615 m, *Steyermark* 60844 (US, holotype; BM, isotype) (the only specimen seen).

Geographical range: Known only from south-east Venezuela.

Note: Pubescence on the surface of the leaves is very rare in *Selaginella.* It is known in *S. hispida* (Willd.) Sw. from Jamaica, *S. plagiochila* Baker from Cuba, *S. trachyphylla* A. Br. from southern China, and *S. tyleri* (No. 52) from Venezuela.

20. Selaginella bahiensis Spring in Martius, *Fl. Bras.* **1** (2) : 124 (1840). Type from Brazil, Bahia: *Blanchet* 2528 (G, P).

Two subspecies are recognised:
Subsp. **bahiensis**

Specimens seen:
BRAZIL. Bahia: type as above; *Blanchet* s.n. (BM), 549 (G, NY); Soteropolis, *Blanchet* s.n. (G); Igregavelha, *Blanchet* s.n. (P); forests of Rio Grongoy basin, *Curran* 290 (B).

Geographical range: Recorded only from eastern Brazil.

Subsp. **manausensis** (Bautista) Jermy & Rankin, **comb. nov.**
Basionym: *Selaginella manausensis* Bautista in *Bolm Mus. Para. Emilio Goeldi* (Bot.) II, **45** : 2 (1974). Type from Brazil, Amazonas: along road from Manaus to Itacoatiara, at km 64, *Rodrigues, Coelho & Monteiro* 8588 (INPA, holotype; MG, isotype).

Geographical range: Known only from the type.

Notes: We could see only minor differences between Dr Bautista's plant and the type of *S. bahiensis*; the former has narrower, lanceolate-elliptic, denticulate, median leaves with an acute apex, compared with the obovate-elliptic, more coarsely toothed leaves, with an acuminate, even aristate apex, of subsp. *bahiensis.* We believe the two are closely related, but because of the geographical separation, accord them subspecific rank.

21. Selaginella wolfii Sodiro, *Crypt. Vasc. Quito* : 620 (1893). Type from Ecuador: woods of the western region, 1800 m, *Sodiro* s.n. (P).

Specimens seen:
COLOMBIA. Chocó: Bahia Solano, *Haught* 5525 (BM). Caldas: above Armenia, 1300—1500 m, *Pennell, Killip & Hazen* 8717 (BM, NY). Valle del Cauca: Queremal, Dagua, *Perez* 3207 (BM); 1300 m, *Alston* 7907 (BM); Cordona, 80–100 m, *Killip* 5031 (NY, US), 5046 (NY, US); Cisneros, 300–500 m, *Killip* 11489 (NY, US); valley of R Dagua, near sea level, *Alston* 8652 (BM); 900 m, *Alston* 7810 (BM); 950 m, *Alston* 7801 (BM); 1000 m, *Alston* 7896 (BM). Nariño: Pambana, above Barbacoas, 50 m, *Ewan* 16842 (BM).
ECUADOR. Without exact locality: type as above. Pastaza: southern border of Rio Napo, 2 km W of Yuralpa *Holm-Nielsen & Jeppesen* 995 (AAU).
PERU. Cusco: In the region of Quincemil and Carratera from Cusco to Puerto Maldonado, *Lobin* s.n. (BM).

Geographical range: Colombia and Ecuador, mainly on the western cordillera. The material recently collected in Peru is not typical, but we believe that it is within the range of the species.

22. Selaginella hartii Hieron. in Urban, *Symb. Antill.* **3** : 525 (1903). Type from Trinidad: Tucuche, *Crueger* 181 (TRIN).

Specimens seen:
VENEZUELA. Sucre: peninsula of Paria, Cerro Patao, north of Puerto de Hierro, 850–860 m, *Steyermark & Agostini* 91202 (BM, US).

Geographical range: Trinidad and Venezuela.

23. Selaginella praestans Alston, **nom. nov.**
Selaginella sprucei A. Braun in *Annls Sci. Nat.* (Bot.) V, **3** : 277 (1865), non Hook. (1861). Type from Peru, Loreto: woods of Rio Yacu-catina, Mt Guayrapurima, near Tarapoto, *Spruce* 4788 (G, holotype; BM, NY, isotypes).
Selaginella anceps sensu Baker, *Fern Allies* : 104 (1887), p.p. non (C. Presl) C. Presl (1844).

Specimens seen:
COLOMBIA. Cauca: Chuare, *Haught* 5385 (BM, COL).
ECUADOR. Napo-Pastaza: Mera, *Asplund* 18794 (S); banks of Rio Cotapino, *c.* 1·5 km W of Rac. Cotapino, 360 m, *Whitmore* 728 (BM). Pichincha: Rio Toachi, above confluence with Rio Pilaton, *c.*

915 m, *Bell* 248 (BM); Red-bark woods of Chimborazo, *Spruce* 5676 (BM); Archidona, *Jameson* 766 p.p. (BM).
PERU. Huánuco: Hacienda Mercedes, Cotirarda, 1500 m, *Mexia* 8196 (BM); Tingo Maria, *Asplund* 12239 (S). Loreto: type, as above.

Geographical range: Colombia to Peru.

Notes: Braun cited the type of *S. sprucei* as *Spruce* 4780. This was a misprint, as has been ascertained from the type specimen at Genève.

24. Selaginella amazonica Spring in Martius, *Fl. Bras.* **1** (2) : 124 (1840), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 176 (1850); Baker, *Fern Allies* : 103 (1887). Type from Brazil; without precise locality, *Martius* s.n. (M).
Selaginella rionegrensis Baker in *J. Bot., Lond.* **23** : 117 (1885), *Fern Allies* : 101 (1887). Type from Brazil.

Specimens seen:
VENEZUELA. Amazonas: Cerro de la Neblina, Río Yatua, between camps 2 and 3, 200–600 m, *Maguire, Wurdack & Bunting* 37393 (BM, NY).
COLOMBIA. Amazonas: Raudal de Jirijirimo, R Apoporis, *Schultes* 12083 (BM); *Garcia* 13726 (BM). Vaupés: near Piedra de Cocui, Rio Negro, *Schultes & Lopez* 9523 (BM); Raudal de Jirijirimo, Rio Apoporis, 250 m, *Schultes & Cabrera* 12458 (COL, US); Caño Paca, Raudal Yo-ree-hwe-ro, Rio Piriparaná, *Schultes & Cabrera* 17562 (US), 17570 (US); Cachivera Miriti, 250 m, *Schultes & Cabrera* 14410 (COL, US), 14410c (US); Rio Vaupés, Javareté, *Schultes & Cabrera* 19422 (UC).
BRAZIL. Without precise locality: type as above. Amazonas: S of Serra Cuputy, Rio Uyapurá, Herb. *Capanema* 32764 (BM); near Panure, Rio Uaupés, *Spruce* 2501 (BM, type of *S. rionegrensis* Baker); base of Serra Tukano, above Trovao, Rio Uaupés, *Schultes & Pires* 9005 (BM); Varadouro, Uaupés, *Luetzelburg* 23646 (M); San Gabriel, Cuabrugas, *Spruce* 2358 (K); San Gabriel, *Spruce* 2053 (K); Estrada Campos Salles, Manaos, *Huebner* 67 (B).

Geographical range: Venezuela, Amazonian Brazil and Colombia.

25. Selaginella oaxacana Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 177 (1850). Type from Mexico, Oaxacana: Chinanbla, *Galeottii* 6808 *bis* (BM, P).
Selaginella anceps sensu Baker, *Fern Allies* : 104 (1887); sensu Christ in Pittier, *Primitiae Florae Costaricensis* **3** (1) : 61 (1901); non *Lycopodium anceps* C. Presl.

Specimens seen:
COLOMBIA. Chocó: La Concepción, 15 km E of Quibdo, 75 m, *Archer* 1974 (BM). Cundinamarca: Andes of Bogota, *Triana* s.n. (P). Nariño: Tuquerres road, Barbacoas, 900 m, *Triana* 696 (BM, COL). Valle del Cauca: Cordoba, *Killip* 5092 (US); *v. Sneidern* 4467 (S); Costa del Pacifico, Rio Raposo, 20–50 m, *Idrobo* 5255 (BM).
ECUADOR. Napo-Pastaza: Mera, to approx. 4 km N of the village (along Rio San Jorge and Rio Tigre) 1200 m. *Øllgaard & Balslev* 9074 (AAU, BM). Santiago-Zamora: Cordillera Cutucu, *Camp* E 1194 (BM).

Geographical range: Mexico to Ecuador.

Notes: Alston placed South American material in this species with some reservation. We feel, with the material available, there is no good reason for distinguishing it as a separate taxon.

26. Selaginella quadrifaria Alston, **sp. nov.** (Figs 4 & 5)
Species heterophylla ex affinitate *S. praestantis,* sed foliis intermediis minus inaequilateralibus, foliisque caulium apicem versus magnis, quadrifariis, et magnitudine fere aequalibus, differt.

Planta e basi breviter repente erecta; *caulibus* glabris usque ad 55 cm altis, basi 3 mm in diam; parte inferiore simplici *c.* 32 cm longa, in siccitate pallide straminea, subdistantibus tecta superiorem partem versus foliis majoribus minus aequalibus; rhizophoris basi restrictis; parte frondosa ambitu late ovata, ramis usque ad 4 cm inter se distantibus, bipinnatis,

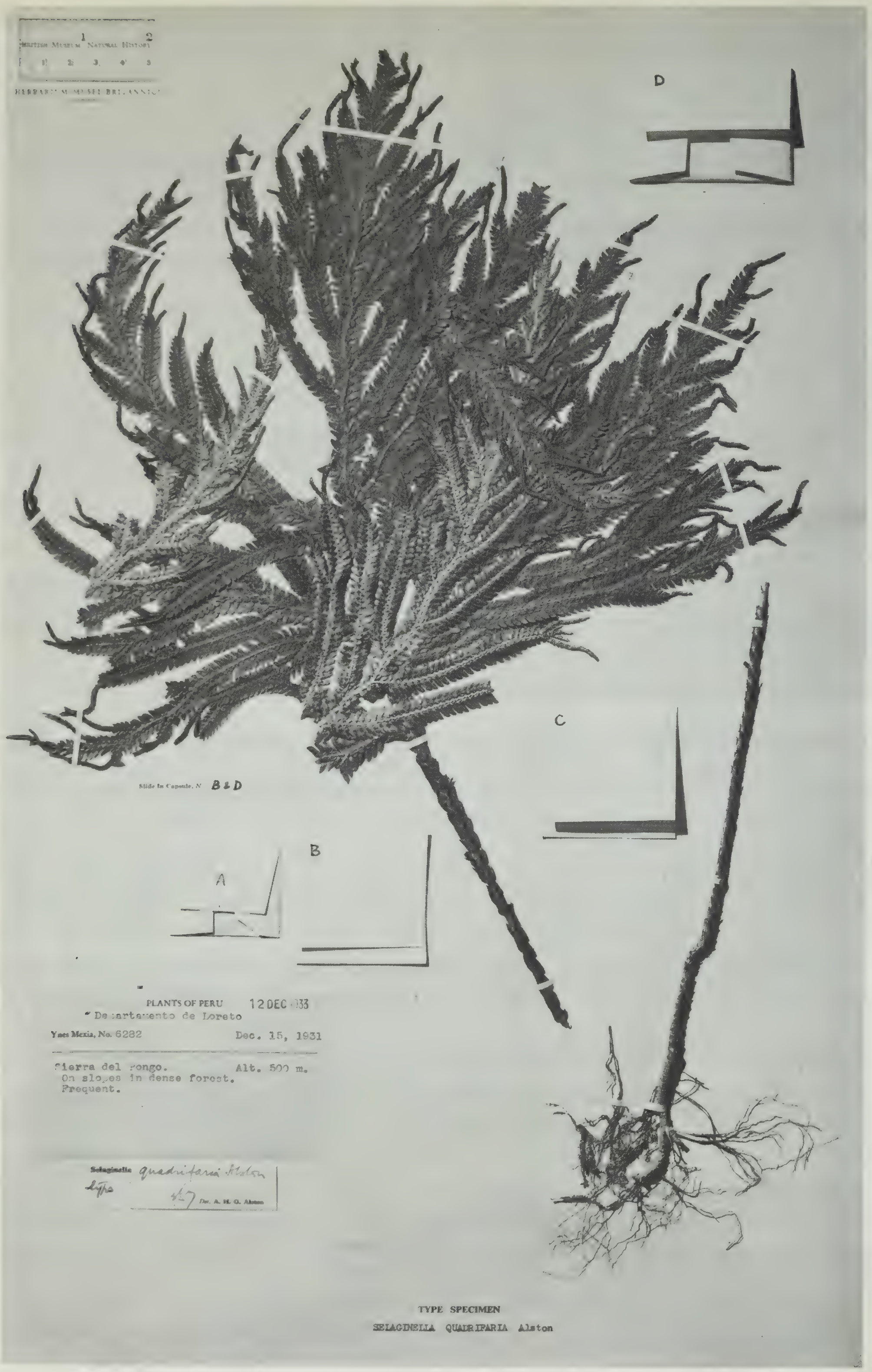

Fig. 4 *Selaginella quadrifaria* Alston: Type specimen, *Mexia* 6282 (BM).

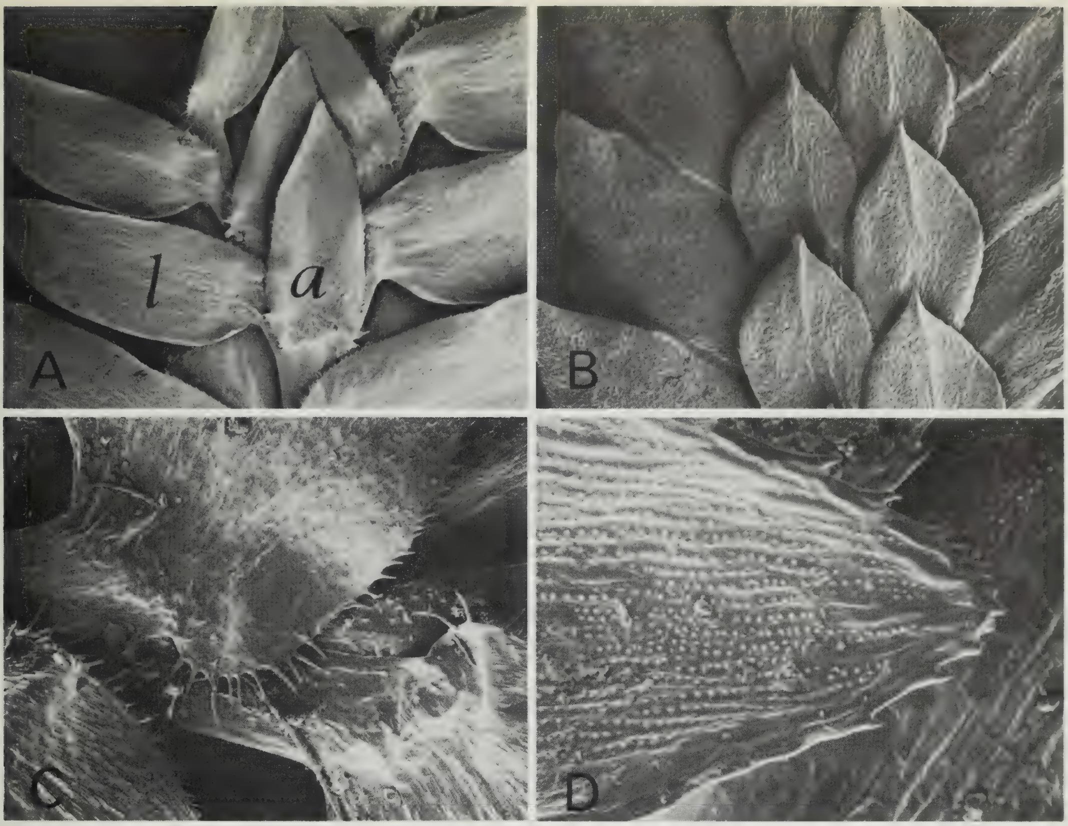

Fig. 5 *Selaginella quadrifaria* Alston: **A.** Close-up of lateral (*l*) and axillary (*a*) leaves, ×8. **B.** Close-up of median leaves, ×8. **C.** Lateral leaf showing acroscopic auricle, ×32. **D.** Apex of lateral leaf, ×224. All from *Mexia* 6282.

ambitu ovatis vel deltoideis, usque ad 20 cm longis, 12 cm latis. *Folia caulium* in parte infima deltoidea, integra, subacuta, 2·5 mm longa, in parte superiore ovata, usque ad 6 mm, serrulata, basi nonnunquam ciliata, apice leviter acuminata; *folia lateralia* partis frondosae fere horizontaliter patentia, leviter imbricata, oblonga, *c.*8 mm longa, 3 mm lata, fere concoloria; semifacie superiore semi-oblonga, basi leviter cordata, et ciliata, alibi serrulata; semifacie inferiore semi-oblonga, basi retracta, attenuata et excavata, integra; *folia axillaria* oblongo-deltoidea, basi utrinque cordata et ciliata; *folia intermedia* oblongo-ovata, 3·5 mm longa, 3 mm lata, divergentia, fere aequilateralia, vix acuminata. *Strobili* in apicibus ramulorum singuli vel bini dispositi, tetragoni, 1·5 cm longi, 2 mm lati, nonnunquam ramosi; *sporophylla* ovato-deltoidea, carinata, serrata, sensim acuminata; *megasporae c.* 400 μm albidae, subtiliter reticulatae; *microsporae c.* 27 μm crassae, pallide lutescentes, papillis elongatis crebre obsitae.

Typus: Peru, Loreto: Sierra de Pongo, 500 m, legit *Mexia 6282* (BM, holotype).

Other specimens seen:
COLOMBIA. Without exact locality: 'Southern', *Hopp* s.n. (B, fragm. BM).
PERU. Junin: Puerto Yessup, 400 m, *Killip & Smith* 26372 (BM, NY).

Geographical range: Southern Colombia to northern Peru.

27. Selaginella tanyclada Alston ex Crabbe & Jermy in *Am. Fern J.* **63** : 143 (1973). Type from Colombia, Chocó: La Concepcion, 15 km E of Quibdo, 75 m, *Archer* 1966 (US, holotype; BM, isotype).

Specimens seen:
COLOMBIA. Chocó: type, as above; Alto de Buey, Nuqui, 1000 m, *Sneidern* s.n. (S).

Geographical range: Confined to Colombia.

28. Selaginella bombycina Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 191 (1850); Baker, *Fern Allies* : 80 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 284 (1950); Alston in *Bull. Br. Mus. nat. Hist.* (Bot.) **1** : 236 (1955). Type from Peru, San Martin: Juana del Rio, *Matthews* 1781 (K).
Selaginella wallisii Regel ex Salom., *Nomencl.* : 358 (1883), nom. nud.
Selaginella anceps sensu Sodiro, *Crypt. Vasc. Quit.* : 621 (1893), non C. Presl.

Specimens seen:
COLOMBIA. Antioquia: Sonson, Rioverde, Rio Verde de los Montes, *Gutierrez* 35629 (UC). Nariño: Costa del Pacifico, Rio Telembi, Barbacoas, 30 m, *Idrobo & Weber* 1459 (BM). Tolima: 'La Trinidad', Libano, 1100–1300 m, *Pennell* 3314 (NY, US). Valle del Cauca: bank of R Engano, Dagua Valley, 700 m, *Alston* 7859 (BM); Cisneros, 300–500 m, *Killip* 35543 (COL).
ECUADOR. Esmeraldas: Playa Rica, Parroquía de Concepción, 105 m, *Mexia* 8434a (BM), 8475 (BM); Angamarca, Leon, *Sodiro* s.n. (NY). Guyas: near Quillallpa, 150 m, *Fagerlind & Wiborn* 679 (S); Teresita, 3 km W of Bucay, 270 m, *Hitchcock* 20484 (BN, NY, US); Tenguel Estate, near Guayaquil, *Haught* 2876 (BM); near Bucay, 300–375 m, *Camp* E3847 (BM). La Paz: Polo-Polo near Coroico, Nordyungas, 1100 m, *Buchtien* 3553 (US). Los Rios: Hacienda Clementina, Cerro Mombe, 600 m, *Asplund* 5551 (S) Pastaza: road Puyo-Macas, 31 km from Puyo, 1100 m, *Øllgaard & Balslev* 9026 (AAU). Santiago-Zamora: near Chupiantza, lower plain of R Upano, 500–700 m, *Camp* E1022 (BM).
PERU. San Martin: type, as above; near Tingo Maria, *Allard* 20416 (BM), 20442 (BM), 20834 (BM), 22194 (BM).

Geographical range: Costa Rica to Peru.

Notes: Øllgaard & Balslev 9026 is a form with most median leaves having a short apical arista; those on the main stem, however, show the more typical aristate leaves. Specimens from Costa Rica *(Standley* 37269) have been identified as *S. wallisii* Regel by O. C. Schmidt; it seems probable, therefore, that this name belongs here.

29. Selaginella radiata (Aublet) Spring in *Bull. Acad. r. Belg.* **10** : 143 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 120 (1850), p.p. excl. pl. orbigniana; Alston in *Reprium Spec. nov. Regni veg.* **40** : 308 (1936), in Pulle, *Fl. Surin.* **1** : 165 (1938). Type from French Guiana, without precise locality, *Aublet* s.n. (BM).
Lycopodium radiatum Aublet, *Hist. Pl. Guian.* **2** : 967 (1775), p.p. excl. syn. Dillen. Type as above.
Lycopodium penniforme Lam., *Encycl.* **3** : 20 (1791), excl. var. *β*. Type from French Guiana.
Stachygynandrum penniforme (Lam.) Beauv., *Prodr. Aéthog.* : 110 (1805). Type as above.
? *Selaginella descrescens* Spring in Van Heurck, *Pl. Nov.* : 28 (1870). Type from Brazil.
Selaginella penniformis (Lam.) Hieron. in *Hedwigia* **58** : 295 (1917). Type as above.
Selaginella haenkeana sensu Spring *Mém. Acad. r. Sci. Lett. Belg.* **24** : 187 (1850), p.p. quoad pl. guian.; Baker, *Fern Allies* : 102 (1887), p.p. excl. syn. *S. dimorpha* Klotzsch.

Specimens seen:
FRENCH GUIANA. Without precise locality: type as above; Herb. *Lamarck* s.n. (P, type of *L. penniforme*); Karouany, *Sagot* 838 (BM, NY).
SURINAM. Without precise locality: *Focke* 1254 (U). Nickerie: Upper Nickerie R, *Tulleken* 333 (L), 510 (L). Suriname: Surinam R, *Tresling* 241 (U).
GUYANA. Essequibo: near Chodikar landing, Acarai Region, *Guppy* 457 (BM); Manicole bog, near Onoro River, *Guppy* 336 (BM).
COLOMBIA. Cundinamarca: Cordillera Oriental, between Sebastopol and Analaima, 2285 m, *Little* 8580 (COL); Cordillera Oriental, at railroad station Tablanca, 40 km W, NW of Bogota, *c.* 2200 m, *Little* 9155 (COL).
BRAZIL. Without exactly locality: *Glaziou* 10213 (C). Matto Grosso: St. Manoel, *Hoehne* 5275 (BM).

Para: Belterra, *Black* 47–976 (BM); Fabrica mata de Najatenua, Rio Moju, *Black* 16330 (BM, IAN, U); Rio Cumina, *Sampaio* 5039 (BM); Barra do Rio Jurnena, *Pires* 3679 (BM); St Antonio de Prata, *Huber* 7044 (BM); Rio Trombetas, near Lake Orapecu, *Traill* 1418 (K); Rio Vermelha, Grute Verde, Tocantima; *Froes* 27011 (BM, IAN); Igarpe Pontanarri, Rio Oiapoque, *Froes* 26007, (BM, IAN).

Geographical range: The Guianas, Colombia and N Brazil.

Notes: A very small but distinct plant from Brazil, Santarem, *Spruce.* 682 and 943 (BM, CGE, GH: syntypes of *S. decrescens* Spring) was considered by Alston (*in sched.*) to be a depauperate form of this species. On further investigation it may turn out to be a distinct species. Aublet quotes '*Lycopodioides radiatum, filicinum, minus et angustius* Dillen., Musc. p. 470, t. 67, no. 7', by which he probably intended '*Lycopodioides denticulatum erectum filicinum, minus et argutius* Dillen., Musc. p. 470, t. 65, no. 7', which was from China and represents *S. moellendorffii* Hieron. (specimen in Oxford (OXF) has been determined by Alston). The name appears to have been confused with *Lycopodioides radiatum dichotomum* Dillen., Musc. p. 474, t. 67, a true *Lycopodium.* It seems best therefore to follow Baker and accept Aublet's specimen, which Baker unfortunately misidentified, as the type.

30. Selaginella speciosa A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 273 (1865); Knox in *Trans. bot. Soc. Edinb.* **35** : 289 (1950). Type from Colombia, Cundinamarca: Bogota, *Cuervo* [herb. *Triana*] s.n. (BM).

Selaginella huberi Christ in *Bull. Herb. Boissier II,* **1** : 73 (1901); Hieron. in *Hedwigia* **43** : 6 (1904). Type from Peru.

Specimens seen:

COLOMBIA. Without precise locality: *Wallis* s.n. (US). Amazonas: Arriba de la desembocadura del rio Loretoyacu, *Duque-Jaramillo* 2333 (COL). Antioquia: without further locality, *Kalbreyer* s.n. (BM); Quebrada San Julian, between Argelia and El Tigre, 2760–2900 m, *Ewan* 15778 (BM). Caldas: Quebrada Pontona, 18 km W of La Dorada, 400 m, *Haught* 2132 (BM). Cundinamarca: type as above.

ECUADOR. Napo-Pastaza: near Canelos, 3–400 m, *Mexia* 6869 (BM); in sylvis Archedoniae, *Jameson* 766 p.p. (BM). Santiago-Zamora: near Mendez, 425–750 m, *Camp* E892 (BM).

PERU. Loreto: near Tarapoto, *Spruce* 4628 (BM, CGE, NY); between Yurimaguas and Balsapuerto, 135–150 m, *Killip & Smith* 28340 (BM, NY); Balsapuerto, 220 m, *Klug* 2921 (BM); Balsapuerto, 150–350 m, *Killip & Smith* 28403 (BM, NY); Sierra del Pongo, 600 m, *Mexia* 6283 (BM); River Huallaga, *Huber* 1547 (P, type of *S. huberi* Christ).

Geographical range: From Colombia to N Peru.

31. Selaginella haenkeana Spring in *Bull. Acad. r. Belg.* **10** : 225 (1843); in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 187 (1850), p.p.; Hieron. in *Hedwigia* **58** : 295 (1917); Alston in *J. Bot., Lond.* **72** : 226 (1934). Type from Peru, 'Cordilleris Chilensibus', *Haenke* s.n. (PR, holotype; B, US, isotypes).

Lycopodium plumosum sensu C. Presl, *Rel. Haenk.* : 79 (1825), non L. (1753).

Selaginella dimorpha Klotzsch in *Linnaea* **18** : 523 (1844). Type as above.

Selaginella leptoblepharis A. Braun in *Annls Sci. nat* (Bot.) V, **3** : 279 (1865). Syntypes from Colombia.

Selaginella hartwegiana var. *leptoblepharis* (A. Braun) Baker in *J. Bot., Lond.* **23** : 118 (1885), *Fern Allies* : 102 (1887).

Specimens seen:

COLOMBIA. Caldas: Rio Santa Rita, Salento, 16–1800 m, *Killip & Hazen* 8958 (NY). Cundinamarca: Salto de Tequendama, 2100 m, *Triana* s.n. (BM, syntype collection of *S. leptoblepharis* A. Braun); *Lindig* 1506 (BM); *Haught* 6404 (BM); *Holton* 83 (NY); *Alston* 7416 (BM), 7423 (BM); *Joseph* s.n. (US); La Vega, 2400 m, *Lindig* s.n. (BM, syntype collection of *S. leptoblepharis* A. Braun); between La Vega and Facatatioa, 2200 m, *Haught* 6136 (BM); Alban, 1600 m, *Guevara* 305 (US); Cordillera Oriental, falls of Rio Bogota, vicinity of El Salto, *c.* 2500 m, *Little* 7879 (COL); Villete, 800 m *Idrobo & Dumont* 4549 (BM); Salto de Tequendama, 2500 m, *Cuatrecasas* 78 (COL). Santander: Corcoba, near Bucaramanga, 2200 m, *Alston* 7319 (BM). Tolima: 'La Trinidad', Libano 1100–1300 m, *Pennell*

3314A (NY); Ibagué; corregimiento Juntas, finca El Silencio, 2800 m, *Echeverri* 869 (COL). Valle del Cauca: valley of the R Digua, 950 m, *Alston* 7834 (BM); 1050 m, *Alston* 7894 (BM); near Queremal, 1300 m, *Alston* 7905 (BM); banks of Engano, Digua Valley, 700 m, *Alston* 7862 (BM); 'La Gallera', Micay valley, 1400–1500 m, *Killip* 7712 (NY, US), 7765 (NY, US).
ECUADOR. Azuay: Chacanceo, Loma de la Plata, 1430–1465 m, *Steyermark* 52683 (BM); near Portovelo, *Rose* 23450 (NY). Napo: Baeza, *c* 1 km SW of the village 2000 m, *Øllgaard & Balslev* 10215 (AAU).
PERU. Without exact location: type as above; *Matthews* 18 (BM). Junin: Pichis Trail, Dos de Mayo, 1700–1900 m, *Killip & Smith* 25843 (BM, NY); Schunke Hacienda, above San Ramon, 1300–1700 m, *Schunke* A248 (BM, US).
BOLIVIA. Laguna: In antris humidis montium Nuevo Mundo, *Orbigny* s.n. (P).

Geographical range: Colombia, Ecuador, Peru and Bolivia.

Notes: Presl's type in the National Museum at Praha was labelled 'Cordilleras de Chili', but no doubt Haenke collected it in Peru. *Selaginella dimorpha* Klotzsch is an exact synonym of *S. haenkeana* as both were based on *Lycopodium plumosum* sensu Presl.

32. Selaginella hartwegiana Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 188 (1850); Baker, *Fern Allies* : 102 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 256 (1950). Syntypes from Ecuador, Pinchincha: in declivitate Andium prope Nanegal, *Hartweg* 1477 (BM, LG); Tungurahua: in sylvis prope Baños, *Jameson* s.n. (K); ad Pillzhum, *Jameson* s.n. (K).
Selaginella hartwegi Spring ex Benth., *Pl. Hartweg.* : 359 (1857), nom. nud. based on *Hartweg* 1477.
Selaginella lizarzaburui Sodiro, *Crypt. Vasc. Qui.* : 615 (1893). Type from Ecuador.

Specimens seen:
COLOMBIA. Cundinamarca: Villete, 800 m, *Idrobo & Dumont* 4549 (BM). Nariño: near Ricuarte, 1500 m, *Alston* 8434 (BM). Valle del Cauca: near Queremal, 1400 m, *Alston* 7923 (BM).
ECUADOR. Without precise locality: *Jameson* 27 (NY), 106 (BM). Chimborazo: in red-bark woods, *Spruce* 5674 (BM, CGE); near Huigra, *Rose* 23962 (NY); near Las Juntas, *Rose* 23177 (US). Napo-Pastaza: Mera, *Asplund* 19677 (S); Mera, road and mule tracks to *c.* 4 km N of the village, 1200 m, *Øllgaard & Balslev* 9118 (AAU, BM); Baeza-Tena 8 km from Baeza, 1900—2000 m, *Balslev & Madsen* 10368 (AAU); road Baeza-Lago Agrio, Rio Salado, 49 km from Baeza, 1400 m, *Balslev & Madsen* 10280 (AAU, BM). Pichincha: type as above; Saloya, 1800 m, *Acosta Solis* 5626 (BM); El Volante, between Chiriboga and Santo Domingo de los Colorados, *Asplund* 17386 (S); between Quito and Santo Domingo de los Colorados, 1450 m, *Holdridge* 1588 (BM); near Rio Negro, Pastaza Valley, 1250 m, *Diels* 914 (B); Mt Atacazo, near St Florencio, 1600 m, *Sodiro* s.n. (P, type of *S. lizarzaburui* Sodiro); St Florencio, 1600 m André 3632 (NY); Guyas, Hacienda Solento, near Santa Rosa, Canton Pajili, Leon, 1000 m, *Mexia* 6723 (BM); Tungurahua: syntypes as above; between Machai and La Victoria, Rio Pastaza, *Asplund* 8508 (S); Baños, 2000–2400 m, *Lehmann* 361a (BM); between Baños and Cashurco, 1300–1800 m, *Hitchcock* 21869 (NY, US); 2500 m, *Lehmann* 383 (BM).

Geographical range: Colombia and Ecuador.

Notes: Selaginella haenkeana (No. 31) is the closest ally, but has more obtuse and more oblong lateral leaves. *Selaginella hartwegiana* superficially resembles *S. pearcei* (No. 34), which has denticulate (not ciliate) lateral leaves and usually acuminate (not aristate) median leaves. *Selaginella novae-hollandiae* (No. 45) is a smaller species, branched from near the base, with the general outline oblong rather than ovate.

33. Selaginella viticulosa Klotzsch in *Linnaea* **18** : 524 (1844); Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 186 (1850); Baker, *Fern Allies* : 102 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 276 (1950). Type from Venezuela, Federal District: near La Guayra, *Moritz* 70 (BM).

Specimens seen:
VENEZUELA. Without precise locality: *Karsten* s.n. (BM); *Funck* 344 (BM); *Fendler* 258 (NY). Carabobo: Lomas de Turismo, 100–200 m, *Pittier* 13866 (B); San Esteban, near Puerto Cabello, *Alston* 6114 (BM), 6130 (BM); Hacienda Marture, between La Entrada and Las Trincheras, 500 m. *Williams*

& Alston 352 (BM). Federal District: type as above; between Caracas and La Guayra, *Rose* 21725 (NY); Galipan, *Funck* 274 (P).
COLOMBIA. Without exact locality: herb. *A. Braun* s.n. (BM).

Geographical range: Costa Rica and Panama to Colombia and Venezuela.

Notes: Alston collected this species on a wall at Tijuca near Rio de Janeiro in 1938 and believed it to be an escape from cultivation. It is also said to be introduced into Trinidad and Bermuda. The specimen from Colombia without locality (ex hort. Berol. et hb. A. Braun) is a young specimen which lacks a fully developed frond branch system.

34. Selaginella pearcei Baker in *J. Bot., Lond.* **22** : 246 (1884), *Fern Allies* : 75 (1887). Type from Peru, Huanuco: Cordilleras of Pozuzo, *Pearce* 249 (K).
Selaginella oligoclada Baker in *J. Bot., Lond.* **22** : 277 (1884). Type from Colombia.

Specimens seen:
VENEZUELA. Merida: La Mucuy, *Vareschi & Pannier* 1373 (BM); Sierra Nevada, above Merida, 2800 m, *Alston* 6779 (BM). Trujillo : above San Rafael de Bocono, 2500 m, *Box* 3830 (BM).
COLOMBIA. Boyaca: around Bocota, *c.* 2200 m, *Grubb & Guymer* P83 (COL). Cauca: above Carpinteria 2500 m, *Alston* 8217 (BM); W of El Tambo, 2500 m, *Haught* 5209 (BM, COL); Magdalena: near Playoncito, Santa Marta, *Schultze* 1518 (B, BM). Norte de Santander: near Ocaña, 24–2700 m, *Kalbreyer* 1080 (K, type of *S. oligoclada* Baker). Santander: near La Baja, 22–2300 m, *Killip & Smith* 18280 (NY); 3000 m, *Killip & Smith* 18348 (NY).
PERU. Without precise locality: *Matthews* s.n. (BM). Huanuco: type as above. Junin: between S Jose and La Achira, Montanas de Pangoa, *Raimondi* 1563 (B, BM).

Geographical range: Venezuela to Peru.

Notes: Baker (1884) described a specimen from the Andes of Ocaña, Colombia (*Kalbreyer* 1080; K) as *S. oligoclada.* This is a more robust plant with less pinnate branching and with median leaves slightly broader with a distinct cusp. Intermediate forms with *S. pearcei* are found, and it is doubtful if the former species can be maintained. *S. pearcei* may be confused with depauperate non-flagellate specimens of *S. flagellata* (No. 41), but the latter has more attenuate, almost aristate, median leaves.

35. Selaginella meridensis Alston, **sp. nov.** (Fig. 6).
Species heterophylla ex affinitate *S. viticulosae* sed foliis intermediis nec ciliatis nec auriculatis differt.

Planta e basi breviter repente erecta; caulibus glabris, circa 23 cm altis, basi 1·5 mm in diam.; parte inferiore simplici *c.* 9 cm longa, in siccitate pallide virido-straminea, foliis fere ad basin heteromorphis; rhizophoris ad partem basin versus restrictis; parte frondosa ambitu oblonga, ramis usque ad 2·5 cm inter se distantibus, bipinnatis, ambitu irregularibus, usque ad 7 cm longis, 3 cm latis. *Folia lateralia* patentia, fere contigua, oblonga, 5 mm longa, 2 mm lata, subacuta; semifacie superiore semi-oblongo-lanceolata, basi gradatim rotundata, crebre serrata vel plusminusve ciliolata, apicem versus distanter serrata; semifacie inferiore semi-oblonga, basi leviter rotundo-cuneata et ciliolis nonnullis instructa, alibi integra; *folia axillaria* oblongo-lanceolata, serrata, 3·5 mm longa, basi utrinque gradatis rotundata; *folia intermedia* ovato-oblonga, 1·5 mm longa, 1 mm lata imbricata, longe aristata. *Strobili* plerumque in apicibus ramulorum brevium lateralium singuli vel bini dispositi, tetragoni, 3 mm longi, 1·75 mm lati, non ramosi; *sporophylla* deltoidea, carinata, serrulata, vix acuminata; *megasporae c.* 380, pallide flavido-brunneae (humectae), subtiliter reticulatae; *microsporae* papillosae.

Typus: Venezuela, Merida: supra Las Cadras, ad septentriones Torondov, 1820–2255 m, 27 Mar. 1944, *Steyermark* 55791 (BM, holotype; US, isotype).

Other specimens seen:
ECUADOR. Azuay: between Cruz Pamba and Loma de Canela, 2315–2500 m, *Steyermark* 52967 (BM, US). Median, lateral and axillary leaves all lack cilia but in other characters resemble the type.

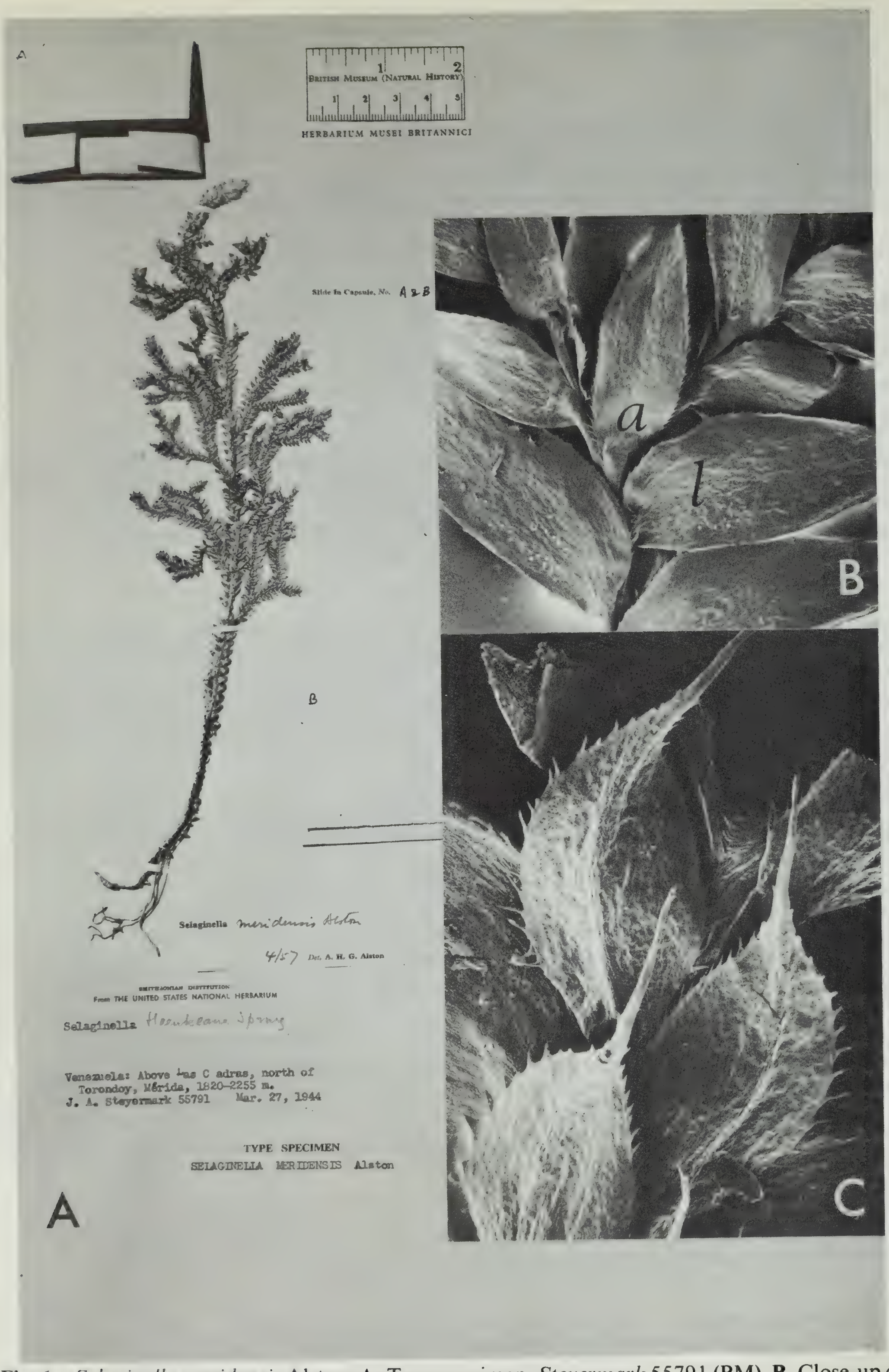

Fig. 6 *Selaginella meridensis* Alston: **A.** Type specimen, *Steyermark* 55791 (BM). **B.** Close-up of lateral (*l*) and axillary (*a*) leaves, × 16. **C.** Close-up of median leaves, × 33. All from *Steyermark* 55791.

Geographical range: Venezuela to Ecuador.

36. Selaginella popayanensis Hieron. in *Hedwigia* **43** : 9 (1904). Type from Colombia, Cauca: near Popayan, *Lehmann* 6968 (US, holotype; K, isotype).
Selaginella moritziana var. *pseudapoda* A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 285 (1865). Type from Colombia.

Specimens seen:
COLOMBIA. Cauca: type as above; Macizo Colombiano, Las Papas paramo, between El Boqueron and La Hoyola, 3200–3510 m, *Idrobo, Pinto & Bischler* 3516 (BM); Purace, km 6, 2750 m, *Alston* 8063 (BM). Cundinamarca: Manzanos, 1700 m, *Lindig* 1518 (BM). Santander: Pamplona, *Joseph* s.n. (BM, US). Valle del Cauca: near Queremal, 1300 m, *Alston* 7906 (BM).
ECUADOR. Carchi: Volcan de Chile, near Tufino, 3630 m, *Wiggins* 10637 (BM). Pichincha: Valley of Lloa, *Benoist* 2700 (P).
BOLIVIA. Without precise locality: *Bang* 80 (BM), 111 (BM), 129 (BM). La Paz: Yungas. *Jay* c (NY), e (NY); 1830 m, *Rusby* 462A (NY).

Geographical range: Colombia to Bolivia.

Notes: As delimited above this species is very variable, and may need further subdivision. *S. cavifolia* (No. 37) differs by having stems which bear rhizophores throughout and relatively broader lateral leaves; *S. flacca* (No. 38) also bears rhizophores throughout. *S. moritziana* (No. 42) bears rhizophores only at the base, but is branched there and is more closely leafy. *S. cruegeri* Jenman from Trinidad is a little known species of similar habit, but with the lateral leaves distinctly ciliolate at the base.

37. Selaginella cavifolia A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 272 (1865); Baker, *Fern Allies* : **43** (1887). Syntypes from Colombia, Cundinamarca: Salto de Tequendanna, *Triana* s.n. (BM); Boquerón, Bogota, 2700 m, *Lindig* 1511 (BM).
Selaginella moritziana var. elongata A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 285 (1865). Syntypes from Venezuela and Colombia.

Specimens seen:
VENEZUELA. Merida: Tovar, *Fendler* 322, 323 (BM; syntypes of *S. moritziana* var. *elongata* A. Braun).
COLOMBIA. Cundinamarca: syntypes as above; Salto de Tequendama, 2100 m, *Alston* 7413 (BM); Bogota, Rio Arz, 2900 m, *Lindig* 1505 (BM; syntype of *S. moritziana* var. *elongata* A. Braun); Laches, 2800 m, *Lindig* s.n. (BM); Sebastopol, Cordillero Oriental 2400 m, *Little* 8611 (COL); falls of Rio Bogota, vicinity of El Salto, 2430–2450 m, *Little* 7897 (COL). Norte de Santander: La Mesita, Pamplona, 2825 m, *Alston* 7236 (BM).
ECUADOR. Along Rio Valladolid, Quebrada Honda and Tambo Valladolid, 2–3000 m, *Steyermark* 54584 (BM).

Geographical range: Venezuela, Colombia and Ecuador, at high elevations.

38. Selaginella flacca Alston, **sp. nov.** (Figs 7 & 8)
Species heterophylla ex affinitate *S. moritzianae* sed differt caulibus ubique rhizophoros gerentibus; habitu laxiore et caulibus flagelliferis.

Planta ubique repens *caulibus* glabris, circa 9 cm longis, filiformibus, basi 0·3 mm in diam., e basi ramosis, in siccitate albido-stramineis, foliis ad basin heteromorphis, rhizophora ubique gerentibus; parte frondosa ambitu oblonga, ramis circa 0·5 cm inter se distantibus, pinnatis, ambitu irregularibus, usque ad 3 cm longis, 1·5 cm latis; *Folia lateralia* patentia, distantia, ovato-elliptica, 2 mm longa, 1·5 mm lata, minute cuspidata; semi-facie superiore semi-ovato-elliptica, basi rotundata, minute ciliato-denticulata, alibi distanter serrata; semifacie inferiore semi-oblongo-elliptica, basi rotundata, distanter et minute serrata; *folia axillaria* lateralibus similia sed minus obliqua; *folia intermedia* elliptica, vel ovato-elliptica, 1 mm longa, 0·7 mm lata, distantia, distanter serrata, apice acuminato. *Strobili* in apicibus ramulis lateralibus singuli dispositi, platystachyi, 5 mm longi, 2·25 mm

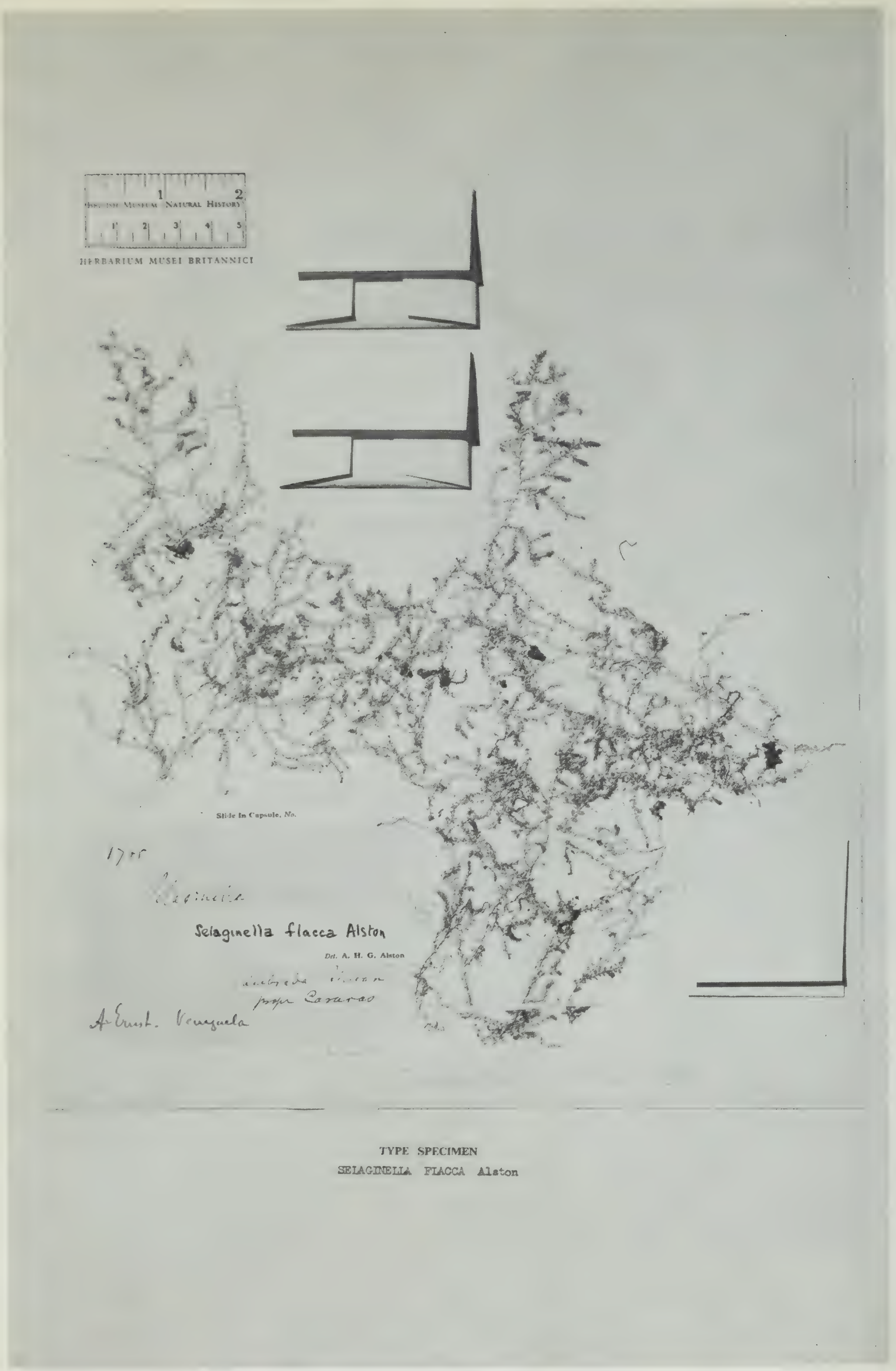

Fig. 7 *Selaginella flacca* Alston: Type specimen, *Ernst* 1765 (BM).

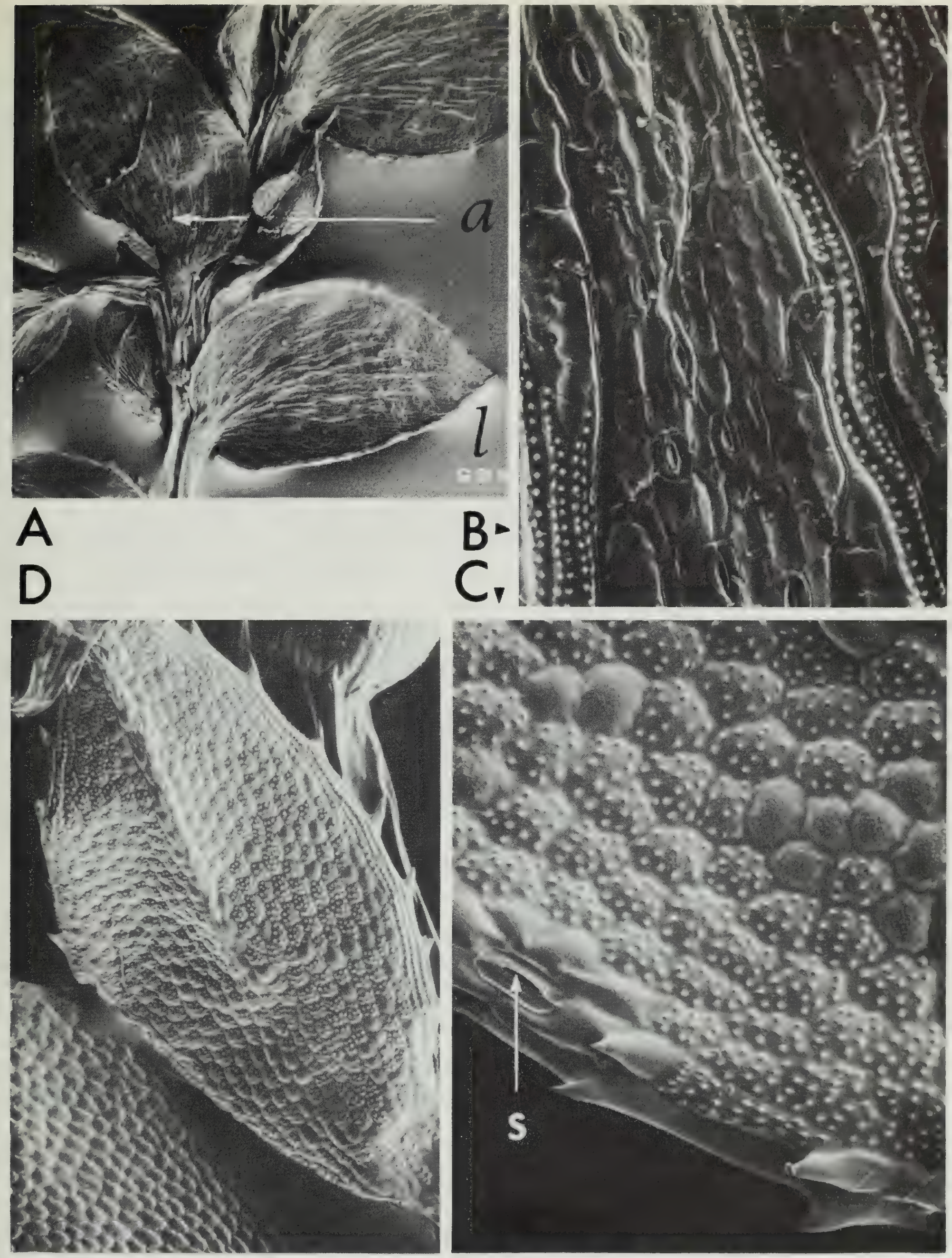

Fig. 8 *Selaginella flacca* Alston: **A.** Close-up of lateral (*l*) and axillary (*a*) leaves, × 18. **B.** Lower epidermis of lateral leaf showing stomata and papillate ridges, × 190. **C.** Upper epidermis of lateral leaf showing stoma (*s*) on margin, × 340. **D.** Close-up of median leaf, × 115. All from *Ernst* 1765.

lati, non ramosi; *sporophylla* dimorpha, dorsalia viridia oblique anguste oblongo-lanceolata, distanter serrata, apice acuto; ventralia hyalina, aequilateralia anguste oblongo-lanceolata, distanter serrata, apice acuminato; *megasporae c.* 325 μm, luteae, laeves; *microsporae c.* 28 μm, luteae (humectae), rugulosae, parce granulosae.

Typus: Venezuela, Miranda: Quebrada Seburan, prope Caracas, *Ernst* 1765 (BM, holotype).

Other specimens seen:
VENEZUELA. Miranda: Galipan, *Moritz* 71 & 221 (BM); Caracas, *Moritz* 71 (BM); Sierra de El Avila, 1675 m, *Steyermark* 55135 (BM, US); Silla de Caracas, *Ernst* 1567a (BM). Sucre : Helvetia, 1730 m, at the mouth of Rio Amana, around Turumiquire, *Nett* 11 (BM).
COLOMBIA. Cundinamarca: Cordillera Oriental, canyon at NE edge of Bogota (E of Calle 72), 2700 m, *Little* 9802 (COL).

Geographical range: The Andean chain of Venezuela and Colombia south to 4°N.

Notes: It appears that the determiner [A. Braun ?] of Moritz collections sorted them into species groups when gatherings were mixed. We therefore find labels bearing '71 & 221', meaning that the material thus distributed with that label came from both field collections.

39. Selaginella macilenta Baker in *J. Bot., Lond.* **22** : 90 (1884); *Fern Allies* : 68 (1887). Type from Ecuador, Chimborazo: at the foot of Mt Chimborazo, 900 m, *Spruce* s.n. (K).

Specimens seen:
COLOMBIA. Santander: Carcoba, near Bucaramanga, 2450 m, *Alston* 7293 (BM).
ECUADOR. Chimborazo: type as above. Pinchincha: by Rio Toachi, above the confluence with the Rió Pilaton, 900 m, *Bell* 227 (BM); Saloya, W side of the Cordillera Occidental, 1800 m, *Acosta Solis* 5790 (BM).

Geographical range: Colombia and Ecuador.

Notes: The type specimen has been mounted with the stems matted together so that the form of the individual plants is difficult to make out, but the species appears to differ from *S. cavifolia* (No. 37), *S. moritziana* (No. 42), and *S. popayanensis* (No. 36) by distinctly aristate median leaves, numerous soboles or terminal flagellae, and narrow sporophylls.

40. Selaginella mollis A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 276 (1865); Baker, *Fern Allies* : 85 (1887). Type from Colombia, Norte de Santander: Ocaña, 1800 m, *Schlim* 1029 (K).

Specimens seen:
COLOMBIA. Antioquia: Rio Mulatos, E of Turbo, 75 m, *Haught* 4957 (BM, COL). Chocó: between Atrato and Truando, *Schott* 8 (BM); between Truando and Nercua, *Schott* 8 (NY). Norte de Santander: type as above.

Geographical range: Mexico to Colombia.

Notes: This species resembles *S. heterodonta* (Desv.) Hieron. of the Greater Antilles, but in that species the median leaves are elliptic-oblong with long cilia, while in *S. mollis* they are nearly round and with short cilia.

41. Selaginella flagellata Spring in *Bull. Acad. r. Belg.* **10** : 228 (1843); in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 207 (1850); Baker, *Fern Allies* : 73 (1887); Alston in *J. Bot., Lond.* **72** : 37 (1934), in Pulle, *Fl. Suriname* **1** : 168 (1938). Type from French Guiana, Inini: source of the Rio Oyapok, *Leprieur* s.n. (LG, holotype; P, isotype).
Selaginella ambigua A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 286 (1865); Baker, *Fern Allies* : 121 (1887). Type from Venezuela.
Selaginella leptostachya A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 289 (1865); Baker, *Fern Allies* : 122 (1887). Type from Colombia.
Selaginella regularis Baker in *J. Bot., Lond.* **22** : 277 (1884); *Fern Allies* : 78 (1887). Type from Peru.
Selaginella rhizophora Baker in *J. Bot., Lond.* **22** : 244 (1884), *Fern Allies* : 73 (1887). Syntypes from Panama.
Selaginella purdiei Hieron. in *Hedwigia* **58** : 322 (1917). Type from Trinidad.

Selaginella othmeri Hieron. in *Hedwigia* **58** : 324 (1917). Type from Trinidad.
Selaginella reptans Sodiro, *Crypt. Vasc. Quit.* : 597 (1893). Type from Ecuador.
Selaginella polysperma sensu Sodiro, *Rescens. Crypt. Vasc. Quitensis.*: 92 (1883), non Spring.

Specimens seen:
GUYANA. Berbice: Sierra Acarai Region, 1/4 mile south of Camp 3, *Guppy* 378 (BM); Manicole bog, 2 miles NE of Camp 1, *Guppy* 336A (BM). Essequibo: Kaietur, *Jenman* ff. (NY).
FRENCH GUIANA. Inini: type as above.
SURINAM. Saramacca: Tafelberg, *Maguire* 24337 (BM).
VENEZUELA. Aragua: Colonia Tovar, *Fendler* 324 p.p. (B; syntype of *S. ambigua* A. Braun); north of Maracay, 900 m, *Box* 3922 (BM); Guamitas, 760 m, *Williams & Alston* 205 (BM), *Alston* 5761 (BM). Bolívar: near Salto de Pacairao, NE of Santa Teresita de Kavanayen. *Steyermark* 60523 (BM). Carabobo: between Carabobo and Tinaquillo, 500 m, *Alston* 5747 (BM); above Hacienda Cura, 1000 m, *Alston* 6291 (BM). Delta Amacuro: Imataca Mountains, *Thompson* 20 (BM). Merida: Santa Cruz de Zamora, 1000 m, *Alston* 6992 (BM). Nueva Esparta: Margarita Island, Pico Blanco, 500 m, *Ginés* 4074 (BM). Sucre: Quebrada del Imposible, Cumana, *Moritz* 221 (B, syntype of *S. ambigua* A. Braun). Yaracuy: Hacienda Iboa, near Guyama, 4–500 m, *Pittier* 11145 (NY, VEN).
COLOMBIA. Boyaca: Beside trail from Bocota to Bachira, on steep north bank of the Rio Royata, *c.* 2050 m, *Grubb & Guymer* P 95 (BM); Muzo Minas Mujo, 700 m, *Lindig* 1514 (BM, type-collection of *S. leptostachya*). Magdalena: near Onaca, 750 m, *Smith* 2245 (BM, NY, US). Meta: Guapayita, Macarena, *Idrobo & Schultes* 833a (BM); Rio Guatriquia near Villa Vicencio, 500 m, *Alston* 7603 (BM). Santander: near Barranca Bermeja, 100–500 m, *Haught* 1970 (BM), 1979 (BM); near Puerto Berrio, 100–700 m, *Haught* 1870 (BM). Valle del Cauca: Rio Engano, Digua Valley, 700 m, *Alston* 7878 (BM).
ECUADOR. Manabi: R Toachi, *Sodiro* s.n. (P, syntype of *S. reptans* Sodiro) San Miguel, *Sodiro* s.n. (P, syntype of *S. reptans* Sodiro). Pichincha: Andes of Quito, *Sodiro* s.n. (P); near Quinide, *Holdridge* 1665 (BM).
PERU. Cuzco: Sapansachayoc, Paucartambo, 900 m, *Vargas* 7360 (BM); near Cuzco, *Jay* a (NY); Quellanu, 900 m, *Bues* s.n. (B). Huanuco: Cueva de las Pavas, 5–600 m, *Ferreyra* 2892 (BM). Junin: Chanchamayo Valley, *Schunke* 189 (BM); E of Quimiri Bridge, La Merced, 700–1300 m, *Killip & Smith* 23945 (BM, NY), 24021 (BM, NY). Loreto: Tarapoto, *Spruce* 3977 (BM, GCE, type collection of *S. regularis* Baker); between Yurimaguas and Balsapuerto 135–150 m *Killip & Smith* 28350 (BM, NY); above Pongo de Manseriche, 220 m, *Mexia* 6366a (BM). San Martin: Juan Jui, Alto Rio Huallaga, 4–800 m, *Klug* 4230 (BM, UC).
BOLIVIA. Cochabamba: Antathuacana, Espiritu Santo, *Buchtien* 2252 (BM); s.n.(Rosenstock exsicc. 98; BM). La Paz: Guanay, *Tate* 557 (NY); Sorata, Larecaja, 300, *Rusby* 203 (NY); Yungas, 1800 m, *Rusby* 453 (NY).
BRAZIL. Amazonas: Bocco de Tejo, Rio Jurua, *Ule* 5524 (K). Matto Grosso: Poaia, Buritzinho, *Lindman* A 3265 (NY).

Geographical range: From Mexico to Bolivia and east to French Guiana and Brazil.

Notes: Braun states that the microspores of his *S. leptostachya* are tuberculate (not papillose); this is true but they appear to be unripe. This species may be separated from *S. cladorrhizans* (No. 43) by its more ovate, acute, cordate leaves. *S. muscosa* (No. 88) has similar leaves, but the strobili are tetragonous; its habit is prostrate and it lacks flagellae. *S. pearcei* (No. 34) is darker green with shortly aristate median leaves, *S. flagellata* being more delicate, paler green with long aristate median leaves. *S. sandwithii* (No. 80) is more erect, lacks flagellae and has tuberculate microspores, whilst those of *S. flagellata* bear elongate papillae as in *S. cladorrhizans.*

42. Selaginella moritziana Spring ex Klotzsch in *Linnaea* **20** : 436 (1847), nom. nud., in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 249 (1850); Baker, *Fern Allies* : 69 (1887), p.p. quoad pl. venezuelensis. Type from Venezuela, Merída: without exact locality, *Moritz* 377 (BM).
Selaginella moritziana var. *normalis* A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 284 (1865). Type as above.

Specimens seen:
VENEZUELA. Federal District: Los Flores, Serra de El Avila, 1600 m, *Alston* 5538 (BM). Merida: type as above.
ECUADOR. Pichincha/Napo-Pastaza: vallée de Lloa (Ungui), *Benoist 2700* (BM).

Geographical range: Northern Venezuela and Ecuador.

Notes: Braun (1865: 283) (under *S. cladorrhizans*) writes of *Fendler* 324 'mixta cum *S. ambigua* et *moritziana*'. *S. cavifolia* (No. 37) from the Tequendama Falls near Bogota, has more obtuse, relatively broader lateral leaves, scarcely acuminate median leaves, and broader sporophylls. *S. macilenta* (No. 39), from 900 m at the base of Chimborazo, appears to differ by narrower, more oblong lateral leaves, and aristate median leaves. *S. potaroensis* (No. 87) has relatively smaller, much tapered, more ovate, unequal-sided median leaves. *S. flacca* (No. 38) has more distant, paler, green lateral leaves, and the stem bears rhizophores throughout. Spring erroneously cited the type as from Colombia.

43. Selaginella cladorrhizans A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 282 (1865); Baker, *Fern Allies* : 72 (1887); Alston in *J. Bot., Lond.* **72** : 37 (1934). Types from Venezuela, Aragua: Colonia Tovar, *Fendler* 324 p.p. (B, BM) and Falcon: San Carlos, *Moritz* 448 (B,BM).

Specimens seen:
FRENCH GUIANA. Podidier: *Leprieur* 166 (K).
VENEZUELA. Anzoátegui: confluence of Rio León and Rio Zumbador, 4–500 m, *Steyermark* 61191 (BM). Aragua: Colonia Tovar, *Moritz* 71? (B): syntype, as above. Carabobo: between Carabobo Tinaquillo, 500 m, *Alston* 5746 (BM); Hacienda Stelling, 700 m, *Alston* 6300 (BM). Delta Amacuro: Imataca Mts, *Thompson* 19 (BM). Falcon: syntype as above. Miranda: Galipan, *Moritz* s.n. (BM); Petare, *Williams & Alston* 213 (BM); between Petare and La Guayrita, 900 m, *Alston* 5469 (BM).
COLOMBIA. Magdalena: Minea, Santa Marta, 600 m, *Smith* 2567 (NY, US). Vaupes: Soratama, between Rio Pacoa and Rio Kananari, *Schultes & Cabrera* 12755 (COL, US).
BRAZIL. Para: Limestone rocks at Trovadore, *Traill* 1436 (K).

Geographical range: Mexico southwards to French Guiana and Brazil, and in Colombia; also recorded for Trinidad.

Notes: A specimen at New York labelled Guiana, *Jenman,* was more probably from Trinidad. It may be necessary to reduce this species to *S. tenella* (Beauv.) Spring of the Antilles. It is similar in habit to *S. lychnuchus* (No. 47), but that species has strongly dimorphous sporophylls.

44. Selaginella porphyrospora A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 286 (1865). Type from Mexico: Vera Cruz, *Sartorius* s.n. (B, BM).
Selaginella bulbifera Baker in *Gdnrs' Chron.* **1867** : 783, 950 (1867). Type from garden material of unknown origin.
Selaginella binervis Liebm. ex Fourn., *Mex. Pl.* : 148 (1872), in syn.
Selaginella albonitens sensu Christ in Dur. & Pittier, *Primit. Fl. Costaric.* **1** 3 : 255 (1896), non Spring.
Selaginella bernoulii Hieron. in *Hedwigia* **41** : 192 (1902). Type from Guatemala.

Specimen seen:
COLOMBIA. Boyaca: beside trail from Bocota to Bachira, on steep north bank of the Rio Royata, *c.* 2050 m, *Grubb & Guymer* P.95 (BM, COL).

Geographical range: Mexico south to Colombia.

45. Selaginella novae-hollandiae (Sw.) Spring in *Bull. Acad. r. Belg.* **10** : 234 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 208 (1850). Type from 'Nova Granada'? [see Notes].
Lycopodium novae-hollandiae Sw., *Syn. Fil.* : 184, 410 (1806). Type as above.
Lycopodium ciliatum Willd., *Sp. Pl.* **5** : 38 (1810), nomen abortivum, non Lam. (1778). Specimen from 'Nova Granada'? [see Notes].

Selaginella increscentifolia Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 106 (1850). Syntypes from Ecuador, Bolivia and Peru.

Selaginella warscewicziana Klotzsch [ex Lauche], *Verz. August. Garten* : 8 (1856), nom. nud.; Kümmerle in *Mag. Bot. Lap.* **13** : 52 (1915), nom. nud.

Selaginella warscewiczii Linden, *Cat. No. 12* : 23 (1857), nom. nud.; Klotzsch ex A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 276 (1865).

Selaginella ciliata (Willd.) A. Braun, *Index Sem. Hort. bot., Berl.* Appendix **1857** : 16 (1857), non Opiz (1823). Type as above.

Selaginella radiata sensu Baker, *Fern Allies* : 86 (1887); Sodiro, *Crypt. Vasc. Quit.* : 614 (1892), non Spring (1843).

Selaginella triuncialis Sodiro, *Crypt. Vasc. Quit.* : 594 (1893). Type from Ecuador.

Selaginella tucumanensis Hieron. in *Bot. Jb.* **22** : 419 (1896). Type from Argentina.

Specimens seen:

VENEZUELA. Carabobo: La Mona, near Chirgua, 700 m, *Alston* 5940 (BM). Merida: between Hacienda Agua Blanca, above La Azulita, and Rio Capaz, 975 m, *Steyermark* 56150 (BM).

COLOMBIA. Antioquia: Amaya, *Daniel* 4250 (BM); near Antioquia, 550 m, *Barclay & Arboleda* 9 (BM). Chocó: Trunado Falls, *Schott* 11 (BM). Cundinamarca: between Pacho and La Palma, 1100 m, *Haught* 6010 (BM, COL); between Villeta and Guaduas, 1000 m, *Haught* 6744 (BM, COL); near Bogota, 1000–1400 m, *Triana* s.n. (BM); Carretera between Santandercito and El Salto, 2200 m, *Pinto, Polidoro & Dumont* 585 (COL). Meta: Villavicencia, 500 m, *Alston* 7613 (BM); Rio Guapaya, 475 m, *Philipson, Idrobo & Fernandez* 1678 (BM); Guapayita, Macarena 5–600 m *Idrobo & Schultes* 833 (BM). Valle del Cauca: Cali, *André* 441 (NY); Cisneros, Dagua Valley, 300–500 m *Killip* 11497 (BM, NY), 35601 (COL); Dagua 700–900 m, *Killip* 5549 (BM, NY); 200–300 m, *Lehmann* 8913 (NY); Rio Engano, Dagua valley, 700 m, *Alston* 7818 (BM), 7879 (BM); Rio Dagua valley, Chorrera, La Elsa, 975 m, *Killip* 34802 (COL); La Margarita, *c.* 760 m, *Killip* 34903 (COL).

ECUADOR. Without precise locality: *Fraser* s.n. (BM); *Lindig* 1517 (BM); Andes of Quito, *Couthouy* 83 (NY); *Jameson* 13 (BM); Nibey (Mbey ?), *Sodiro* s.n. (NY); way to Nanegal, 2200 m, *Mille* s.n. (NY); Niebli, *Andre* 3771 (NY); San Florencio, 1580 m, *Andre* 3771 (NY); San Jose de Toachi, 100 km W of Quito, *c.* 1000 m, *Bell* 190 (BM). Azuay: W of Patal, between Huahualcay and Passas de Pinglion, 2670–3275 m, *Steyermark* 52601 (BM). Bolivar: San Christobal, 1070 m, *Asplund* 8348 (S). Chimborazo: Near Huigra, R. Chanchan, 1350 m, *Camp* E 3131 (BM); 1500–1950 m, *Camp* E 3275 (BM). Pichincha: *Jameson* s.n. (K); Canzacoto, *Sodiro* s.n. (P, ? type, labelled *S. triuncialis* Sod.); Santo Domingo de los Colorados, 900 m, *Holdridge* 1589 (BM); Chaupi-Sagcha, Puluagua, *c.* 1800 m, *Bell* 473 (BM); Nono, 2600 m, *Asplund* 7481 (S). Santiago-Zamora: Above Rio Upano, 585–660 m, *Camp* E 1448 (BM); Macas, Rio Upano, *Asplund* 19817 (S); near Mendez, 570 m, *Camp* E 894 (BM); E 1011 (BM); E 1475 (BM); E 1476 (BM). Tungurahua: *Bell* 828 (BM); between Banos and Rio Verde, *c.* 1650 m, Agoyan, *Asplund* 7598 (S). On border between Loja and Santiago-Zamora: crest of the Cordillera de Zamora, east of Loja, *c.* 3000 m, *Camp* E 81 (BM).

PERU. Amazonas: Chachapoyas, *Mathews* s.n. (BM). Ayacucho: Pampalca, between Huanta and Rio Apurimac, 3200 m, *Killip & Smith* 22227 (BM, NY), 23240 (BM, NY); Aina, between Huanta and Rio Apurimac, 750–1000 m, *Killip & Smith* 23177 (BM, NY), 22545 (BM, NY); Coarrapa, between Huanta and Rio Apurimac, 1500 m, *Killip & Smith* 22364 (BM, NY). Cuzco: Machupicchu, 2400 m, *Herrera* 3475 (BM); *Stafford* 1068 (BM); Torontoy, Urubamba Valley, 2400 m, *Cook & Gilbert* 1190 (US); San Miguel, Urubamba Valley, 1800 m, *Cook & Gilbert* 1004 (US); 1169 (US). Junin: *Mathews* 1084 (BM, NY, US); Huacapistana, 1800 m, *Killip & Smith* 24275 (BM, NY); 10 km SW of San Ramon, 1000 m, *Tryon* 5448 (BM). La Libertad: Otuzco, road to Paranday (Sinsicap), 2600 m, *López* 1044 (BM). Loreto: Balsapuerto, lower R. Huallaga, 350–550 m, *Killip & Smith* 28488 (BM, NY); near Tarapato, *Spruce* 2328 (BM, CGE). Piura: near Ayabaca, 2700 m, *Berry* s.n. (US). Puño: Ollachea, prov. Carabayo, 2500 m, *Vargas* 6914 (BM).

BOLIVIA. Without precise locality: *Bang* 35 (BM); *Bridges* s.n. (BM). Beni: Huachi, head of Rio Beni 540 m, *White* 541 (BM, NY, US). Cochambamba: Lagnillas, over mountains behind Choro in St Elena valley, 3000 m, *Brooke* 6256 (BM); Incachaca (small power station) *c.* 80 mls NE of Cochamba, 2400 m, *Brooke* 6673 (BM). La Paz: near La Paz, 3000 m, *Rusby* 453 (NY, US); 3600 m, *Rusby* s.n. (BM); Queliquaya, Sorata, Larecaja, 2700 m, *Mandon* 1530 (BM, NY); Hacienda Simaco on way to Tipuam, 1400 m, *Buchtien* 5277 (US), 5278 p.p. (US), 5279 (US); Yungas, *Bang* 440 (BM, NY); 1200 m, *Rusby* 203 (NY); Paradiso, 1350 m, *Williams* 1402 (NY, US). Santa Cruz: Samaipata, 1800 m, *Steinbach* 3740 (BM). Tarija: Pinos, near Tarija 2300 m, *Fiebrig* 2978 (BM).

Geographical range: Nicaragua southwards to Bolivia.

Notes: S. novae-hollandiae is one of the commonest species of *Selaginella* in South America. It is very variable in the density and length of cilia on the leaves. *S. brevifolia* (No. 79) is distinguished by its more prostrate habit, with rhizophores above the middle, and a prominent central ridge on the upper surface of the stem in dried specimens; in *S. novae-hollandiae* there are usually two ridges which are less distinct; furthermore the median leaves of *S. brevifolia* are exauriculate. *S. leucoloma* (No. 58) is similar in habit, but the median leaves are acute (not aristate), exauriculate and more conspicuously white-margined. *S. popayanensis* (No. 36) is separable by its dentate leaves; those of *S. novae-hollandiae* have some long cilia at the base, and are concave below when dry, being strongly cordate and overlapping the stem. *S. radiata* (No. 29), with which it has been confused in the past, is a larger plant with more rounded long-aristate median leaves, and lateral leaves which are more silvery beneath. The type specimens of *Lycopodium novae-hollandiae* Sw. and *L. ciliatum* Willd. were both localised 'Nova Hollandia', perhaps a mistake for Nova Granada (Colombia), as Australia is certainly not implied. There is a specimen at Paris from Canzacito, labelled *S. triuncialis* Sodiro, but the type locality was on the slopes of Mt Atacatzo, Ecuador. It seems to be a small form of *S. novae-hollandiae.*

46. Selaginella chionoloma Alston ex Crabbe & Jermy in *Am. Fern J.* **63** : 137 (1973). Type from Peru, Cuzco: Valle de Lares, Calca Cuquipata, *Herrera* 1636 (US, holotype; BM, isotype).

Specimens seen:
COLOMBIA. Caqueta: Florencia, *Arbelaez* 627 (BM, US).
PERU. Cuzco: type, as above. San Martin: beyond Las Palmas, near tunnel, Tingo Maria, 800 m, *Allard* 21130 (BM).
BOLIVIA. La Paz: Yanacachi, Yungas, *Jay* b (US).

Geographical range: Colombia and Peru to north-western Bolivia.

Notes: This species resembles *S. ramosissima* (No. 48) in general appearance, but that species has a stouter stem and lacks soboles and the conspicuous white margin of the lateral leaves, which is a feature of *S. chionoloma.* It is most closely related to *S. novae-hollandiae* (No. 45), differing only in its lack of definite cilia on the lateral leaves, its more pronounced white border, especially on the acroscopic edge of those leaves, and its narrower median leaves. Pierre Jay's specimen is very poor, but seems to be this species.

47. Selaginella lychnuchus Spring [ex Klotzsch in *Linnaea* **20** : 435 (1847), nom. nud.], in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 247 (1850); Baker, *Fern Allies* : 121 (1887). Syntypes from Venezuela, Federal Dist.: Galipan, *Moritz* 71^2 (B, BM, LG); Merida, *Moritz* 378 (B, BM, LG).

Selaginella lychnuchus var. *flaccida* Spring [ex Klotzsch in *Linnaea* **20** : 436 (1847), nom. nud.], in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 248 (1850). Type as above (*Moritz* 71^2).

Selaginella lychnuchus var. *rigidiuscula* Spring [ex Klotzsch in *Linnaea* **20** : 436 (1847), nom. nud.], in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 248 (1850). Type as above (*Moritz* 378).

Selaginella lychnuchus var. *pusilla* A. Braun in *Annls Sci. Nat.* (Bot.) V, **3** : 288 (1865). Type from Venezuela.

Specimens seen:
VENEZUELA. Aragua: below Rancho Grande, 1000 m, *Williams & Alston* 144 (BM); near La Regriesiva, km 25, 1000 m, *Williams & Alston* 170 (BM). Federal District: syntype, as above. Merida: syntypes as above; Rio Albariga, 2400 m, *Alston* 6969 (BM). Sucre: Quebrada del Impossible, *Moritz* 221 & 71 (BM).
COLOMBIA. Santander: Corcoba near Bucaramanga, 2200 m, *Alston* 7311 (BM).

Geographical range: Costa Rica to Colombia and Venezuela.

Notes: There is some confusion over Moritz's field numbers, and the reason for double numbers is not clear; but there is no ambiguity. There is no doubt that the gatherings were mixed [see *S. cladorrhizans* (No. 43), *S. flacca* (No. 38), *S. flagellata* (No. 41) and *S. pallescens* (No. 5)], and the double numbers may have arisen when Spring or Moritz (or A. Braun?; see p. 272) were sorting them out. On original labels (at least at BM) the two numbers are linked by an ampersand (&).

Three specimens of Moritz are cited here, although Spring (l.c.) only cites two and those as varieties which are solely habitat forms and extremes of the morphological range. Spring gives Colombia as the locality, in error.

48. Selaginella ramosissima Baker in *J. Bot., Lond.* **23** : 295 (1885); Baker, *Fern Allies* : 12 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 260 (1950). Type from Peru, Loreto: near Tarapoto, *Spruce* 4088 (K, holotype; BM, CGE, NY, isotypes).

Specimens seen:
ECUADOR. Santiago-Zamora: between Rio Sabamba and Canillones Tambo, 1300–2100 m, *Camp* E 66 (BM).
PERU. Cajamarca: Monte Seco, Hualgayoc, 1800 m, *Soukup* 3872 (BM). Loreto: type as above.

Geographical range: Ecuador to Peru.

49. Selaginella glossophylla Alston ex Crabbe & Jermy in *Fern Gaz.* **11** : 259 (1976). Type from Bolivia, Cochabamba: Incachaca, 80 miles NE of Cochabamba, 3000 m, *Brooke* 6783 (BM).

Specimens seen:
CHILE. Without exact locality: *Mercier* s.n. (P).
BOLIVIA: type as above.

Geographical range: Bolivia and Chile.

50. Selaginella minima Spring in *Bull. Acad. r. Belg.* **10** : 139 (1843); *Mém. Acad. r. Sci. Lett. Belg.* **24** : 86 (1850); Baker, *Fern Allies* : 84 (1887). Type from French Guiana: ad basin montis Eigre Insulae Cayenne, *Leprieur* 158 (G, K, P, US). Only specimen seen.

Geographical range: Costa Rica, Panama, French Guiana.

Notes: This species is somewhat doubtfully distinct from *S. broadwayi* Hieron., described from Trinidad, and *S. simplex* (No. 51). In *S. broadwayi* the lateral leaves are not ciliate, but otherwise similar; in *S. simplex* the lateral leaves are ovate and denticulate. The three species may form a cline.

51. Selaginella simplex Baker, in *J. Bot., Lond.* **23** : 293 (1885), *Fern Allies* : 121 (1887). Type from Brazil, Para: near Santarem, *Spruce* 947 (BM, CGE, K).

Specimens seen:
VENEZUELA. Carabobo: La Mona, near Chirgua, 700 m, *Alston* 5959 (BM).
BOLIVIA. Near Santa Cruz, *Williams* 2657 (BM, NY, US). Goias: Cerrado 8 km S of Cristalina 1200 m, *Irwin, Grear, Souza & Reis dos Santos* 13654 (BM).
BRAZIL. Para: Type as above. Ceara: Cedro, *Loefgren* 1160 (BM); Pernambuco: Tapera, wall of ditch, *Pickel* 2812 (BM).

Geographical range: Trinidad, Venezuela, Bolivia, Brazil.

52. Selaginella tyleri A. C. Smith in *Bull. Torrey bot. Club* **58** : 311 (1931). Type from Venezuela, Bolivar: slopes of ridge 24, Mount Duida, 1680 m, *Tate* 463 (BM [fragment], NY). Only specimen seen.

Geographical range: Confined to Mt Duida.

53. Selaginella cruciformis Alston ex Crabbe & Jermy in *Fern Gaz.* **11** : 257 (1976). Type from Venezuela, Carabobo: Rio Aguada, 1500 m, *Alston* 64240 (BM, holotype; AAU, COL, INPA, QCA, RB, SP, U, USM, US, VEN, isotypes).

Specimens seen:
VENEZUELA. Aragua: Rancho Grande, 1400 m, *Box* 3879 (BM); *Tschudi* 64 (US). Carabobo: type as above. Merida: prope Tovar, 900 m, *Fendler* 487 (BM). Yaracuy: Cerro La chapa, north of Nirgua, 1200–1400 m, *Steyermark, Bunting & Wessels-Boer* 100259 (BM, US).

Geographical range: Confined to Venezuela.

Notes: This species resembles *S. chrysoleuca* (No. 55) in the sessile lateral strobili and the basal rhizophores. It might also be confused with *S. truncata* (No. 94), but that species is prostrate, rooting throughout, and has terminal strobili.

54. Selaginella acanthostachys Baker in *J. Bot., Lond.* **21** : 99 (1883), *Fern Allies* : 44 (1887). Type from Peru, Loreto: Monte Campana, *Spruce* 4328 (K).

Specimens seen:
ECUADOR. Santiago-Zamora: Valley of R. Negro, down to R. Pailas, *Camp* E 4952 (BM); Cordillera de Zamora, Loja, 3000 m, *Camp* E 80 (BM).
PERU. Cajamarca: Tambillo, Cutervo, 2190 m, *Raimondi* 6791 (BM). Loreto: Type as above.

Geographical range: Ecuador and Peru.

55. Selaginella chrysoleuca Spring in *Bull. Acad. r. Belg.* **10** : 226 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 197 (1850); A. Braun in *Annals Sci. nat.* (Bot.) V, **3** : 274 (1865); Baker, *Fern Allies* : 81 (1887). Type from Bolivia, without precise locality, *D'Orbigny* s.n. (P).
Selaginella sprucei Hook., *Second Cent. Ferns* t.83 (1861). Type from Peru.

Specimens seen:
VENEZUELA. Aragua: near Puerto Cabello, *Karsten* s.n. (B).
COLOMBIA. Santander: Mesa de los Santos, 1500 m, *Killip & Smith* 15211 (B, BM, NY, US); Coromoro, ENE of Charala, 2300 m, *Ewan* 15664 (BM).
ECUADOR. Santiago-Zamora: between Rio Ontza and Chupiasa, Cordillera Cutucu, 1250–1300 m, *Camp* E 1196 (BM); SW of Rio Itzintza, Cordillera Cutucu, 1500–1600 m, *Camp* E 1388 (BM).
PERU. Junin: Pichis trail, Porvenir, 1500–1900 m, *Killip & Smith* 25951 (NY, US). Loreto: Mt Campana, near Tarapoto, *Spruce* 4623 (BM, CGE, K; type of *S. sprucei*); between Tingo Maria and Pucallpa, *Ferreyra* 1008 (BM).
BOLIVIA. Without precise locality: type as above. La Paz: Lower Rio Pelichuco, Caupolican, 1200 m, *Williams* 2647 (NY, US); Santa Barbara, Caupolican, 1650 m, *Williams* 1395 (NY, US); Hacienda Simaco, on way to Tipuani, Larecaja, 1400 m, *Buchtien* 5274 (BM, NY, US); Polo-Polo near Coroica, N Yungas, 1100 m, *Buchtien* 3549 (US).

Geographical range: Venezuela to Boliva.

Notes: The habit of this species resembles that of *S. cruciformis* (No. 53); but the median leaves on the former are falcate with apices crossing one another, and those of the latter subacute with the apices directed forwards. The specimens from Colombia and Venezuela are smaller and perhaps represent a distinct species.

56. Selaginella contigua Baker in *J. Bot., Lond.* **22** : 295 (1884), *Fern Allies* : 79 (1887); Hieron. in *Hedwigia* **43** : 44 (1903). Syntypes from Brazil, Rio de Janeiro, *Glaziou* 4493 (C, K) and Itatiaia, *Glaziou* 5638 (C, K).
Selaginella callimorpha Silveira in *Bolm Comm. geogr. geol. Minas Geraes* **5** : 121 (1898). Type from Brazil.
Selaginella wettsteinii Hieron. in *Denkschr. Akad. Wiss. Wien* **79** : 60 (1908). Type from Brazil.

Specimens seen:
BRAZIL. Without exact locality: *Glaziou* 5216 (C), 5613 (P); Porta d'Estrella el Mandioca, *Beyrich* s.n. (BM). Minas Gerais: Rio Novo, *Capanema* s.n. (BM); Serra de Bocaivra, *Schwacke* s.n. (BM). Parana: *Schwacke* s.n. (BM). Rio de Janeiro: syntypes as above; *Glaziou* 9312 (C, K, P), 9314 (C, K); *Mosen* 53 (K); Tyuca, *Hoehne* 24876 (P, S); *Glaziou* 4676 (C, P); *Lutz* 1151 (BM); Alto da Boa Vista de Nova Friburgo, *Glaziou* 7283 (BM); Mt Itatiaya, 800 m, *Smith* 1638 (C); Itatiaia, *Rose & Russell* 20600 (NY); Itatiaia, Angra dos Rios, Maromba, *Brade* 14530 (BM), 14531 (BM); Serra do Itatiaia, 100 m, *Brade* 6506 (BM); *Dusen* 708 (BM, P); *Sampaio* 4052 (BM); Represa Camorima, *Brade* 12564 (BM); Santa Catarina : Joinville, *Muller* 133a (NY). São Paulo: Serra do Cubata, *Guillemin* 578 (P); Santos, *Mosen* 3556 (K), 3814 (C); *Edwall* 164 (BM); *Rose & Russell* 21128 (NY); ?Jap-nyba, *Hoehne & Gehrt* s.n. (BM); Alto da Serra, *Wacket* 20997 (BM, P); Campo Grande, Sera do Mar, *Brade* 6600 (NY); S. José de Barreiro, *Loefgren & Edwall* 20991 (BM, P); Brasso near Itapecirica, 1000 m, *Wettstein & Schnifner* s.n. (W, type of *S. wettsteinii* Hieron.); Iguape, 800 m, *Brade* 8628 (BM); Serra da Bocaina, *Schwacke & Glaziou* s.n. (BM); Itatinga, *Brade* 10047 (BM), 10264 (BM).

Geographical range: Confined to south-eastern Brazil.

Notes: S. callimorpha A. Silveira was reduced to synonymy by Hieronymus in *Hedwigia*, **43** : 44 (1904); we have not seen the type.

57. Selaginella mendoncae Hieron. in Engl. & Prant, *Nat. Pflanzenf.* **1** (4) : 693 (1901), in *Hedwigia* **45** : 43 (1904). Type from Brazil, Rio de Janeiro, *Mendonça* 302 (K).

Specimens seen:
BRAZIL. Without exact locality: *Glaziou* 7283 (C). Rio de Janeiro: type as above; *Glaziou* 12294 (BM, C, K).

Geographical range: Apparently confined to the area around Rio de Janeiro.

58. Selaginella leucoloma Alston ex Crabbe & Jermy in *Fern Gaz.* **11** : 262 (1976). Type from Bolivia, La Paz: Hacienda Simaco near Tipuani, Larecaja, 1400 m, *Buchtein* 5280 (BM, holotype; US).

Specimens seen:
BOLIVIA. La Paz: Peluchuco *Weddell* 4779 (P); type as above and same locality, *Buchtein* 5278A (BM, US).

Geographical range: Endemic to Bolivia.

Notes: In habit resembles *S. popayanensis* (No. 36), but has ciliate, obtuse, lateral leaves.

59. Selaginella xiphophylla Baker in *J. Bot., Lond.* **22** : 296 (1884), *Fern Allies* : 80 (1887). Type from Peru, Loreto: Mt Guayrapurima, near Tarapoto, *Spruce* 3990 (K, holotype; BM, CGE, NY, isotypes). Only specimen seen.

Geographical range: Confined to Mt Guayrapurima, Peru.

60. Selaginella substipitata Spring in *Bull. Acad. r. Belg.* **10** : 227 (1843); Baker, *Fern Allies* : 58 (1887). Type from Guadeloupe, *Beaupertius* s.n. (? BR, not seen).

Selaginella rigidula Baker in *J. Bot., Lond.* **22** : 295 (1884), *Fern Allies* : 79 (1887). Type from Colombia.

Selaginella karsteniana A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 288 (1865); Baker, *Fern Allies* : 122 (1887). Type from Venezuela.

Specimens seen:
VENEZUELA. Without precise locality: *Karsten* s.n. (BM); Aragua: La Regresiva, 1000 m, *Williams & Alston* 171 (BM). Bolívar: Ptari-Tepui, 2400—2410 m, *Steyermark* 59604 (BM). Carabobo: Puerto Cabello, *Karsten* 174 (B, type of *S. karsteniana* A. Braun).
COLOMBIA. Caldas: Rio Santa Rita, Salento, 1600–1800 m, *Killip & Hazen* 8959 (NY). Santander: Ocaña to Pamplona, *Kalbreyer* 972 (K, type of *S. rigidula* Baker).

Geographical range: Confined to the cordillera in northern Colombia and Venezuela.

61. Selaginella scalariformis A. C. Smith in *Bull. Torrey bot. Club* **58** : 314 (1931). Type from Venezuela, Amazonas: Gorge of Cano Negro, Savanna Hills, Duida, 1200 m, *Tate* 817 (NY, holotype; BM, K, fragment).

Specimens seen:
VENEZUELA. Amazonas: type, as above; summit of Cerro Duida, 1025–1200 m, *Steyermark* 58223 (BM). Bolivar: N Ridge escarpment of Mt Roraima, 1980 m, *Edwards* KER61 (BM, K).

Geographical range: Confined to the sandstone mountains in the south of Venezuela, and only recently discovered on Roraima in 1978.

62. Selaginella wurdackii Alston, **sp. nov.** (Fig. 9)
Species heterophylla ex affinitate *S. roraimensis*, sed foliis intermediis brevissime aristatis, sporophyllis lanceolato-deltoideis, rhizophoris brevibus filiformibus et caulibus brevioribus differt.

Planta ascendens; *caulibus* glabris, circa 5 cm altis, basi 0·6 mm in diam., parte inferiore simplici *c.* 15 mm; rhizophoris ad quartam partem basin versus restrictis; parte ramosa ambitu irregulariter ovato-elliptica, ramis *c.* 5 mm inter se distantibus, simplicibus vel furcatis, usque ad 15 mm longis. *Folia* ubique heteromorpha; *folia lateralia* patentia, distantia oblonga 2 mm longa, 1 mm lata, subacuta; semifacie superiore semi-elliptico-oblonga, basi rotundato-cuneata, integra; semifacie inferiore, semi-oblonga, basi cuneata, apicem versus distanter serrulata, aliter integra; *folia axillaria* minus inaequilateralia sed aliter lateralibus similia; *folia intermedia* ovato-oblonga, 1 mm longa, 0·75 mm lata, serrata, apice breviter aristato. *Strobili* in apicibus ramulorum, singuli vel bini dispositi, tetragoni, 4–12 mm longi, 1·8 mm lati non ramosi; *sporophylla* lanceolata, carinata, distante serrulata, apice leviter attenuato, acutoque; *megasporae c.* 230 μm, luteae (humectae), reticulorugosae; *microsporae c.* 25 μm luteae (humectae) verrucosae.

Typus: Venezuela, Bolivar: between 'La Laja' Base Camp, Rio Tirica, Chimantá Massif, 485–490 m, *Steyermark & Wurdack* 173 (BM, holotype; US, isotype).

Other specimens seen:
VENEZUELA. Bolivar: near Salto de Pacairo, NE of Santa Teresita de Kavanayén, 1220 m, *Steyermark* 60499 (BM).

Geographical range: Known only from south-east Venezuela.

63. Selaginella seemannii Baker in *J. Bot., Lond.* **21** : 244 (1883), *Fern Allies* : 57 (1887); Alston in Pulle, *Fl. Suriname* **1** : 168 (1938). Type from Colombia, Choco: Cacagual Is., *Seeman 1006* (K, holotype; BM, isotype).

Selaginella barbacoasensis Hieron. in *Hedwigia* **43** : 46 (1904), in Engler, *Bot. Jarhb.* **34** : 580 (1905). Type from Colombia.

Specimens seen:
SURINAM. Nickerie: Upper Sipaliwini R., Camp 19, Morro Grande, *Rombouts* 489 (BM).
COLOMBIA. Boyaca: Sierra Nevada de Cocuy, in moss forest around Cobugon, *c.* 2900 m, *Grubb & Guymer* P 57 (COL). Choco: type as above; Mariño: near Barbacoas, *Lehmann* 89 (BM, type collection of *S. barbacoasensis* Hieron.); *Alston* 8509 (BM). Norte de Santander : camp 84 on pipeline, 540 m, *Foster* 1722 (COL.). Valle del Cauca: Bridge over Dagua, near Buenaventura, *Alston* 8632 (BM).
ECUADOR. Napo-Pastaza: near Canelos, 300—400 m, *Mexia* 6906a (BM). Santiago-Zamora; above Rio Chupiantza, 585–660 m, *Camp* E 1444 (BM); above Rio Upano, near Mendez 325–750 m, *Camp* E 972 (BM); Cordillera Cutucú, 1050–1110 m, *Camp* E 1225 (BM).
PERU. Loreto: Rio Itaya, *c.* 10 km S of Iquitos, *Tryon* 5195 (BM); along R. Itaya, *Williams* 238 (BM); Soledad, Rio Itaya, 110 m, *Killip & Smith* 29638 (NY, US); between Manseriche and mouth of the Rio Morona, 150 m, *Killip, Smith & Dennis* 29141 (US).

Geographical range: Colombia east to Surinam and south to Peru.

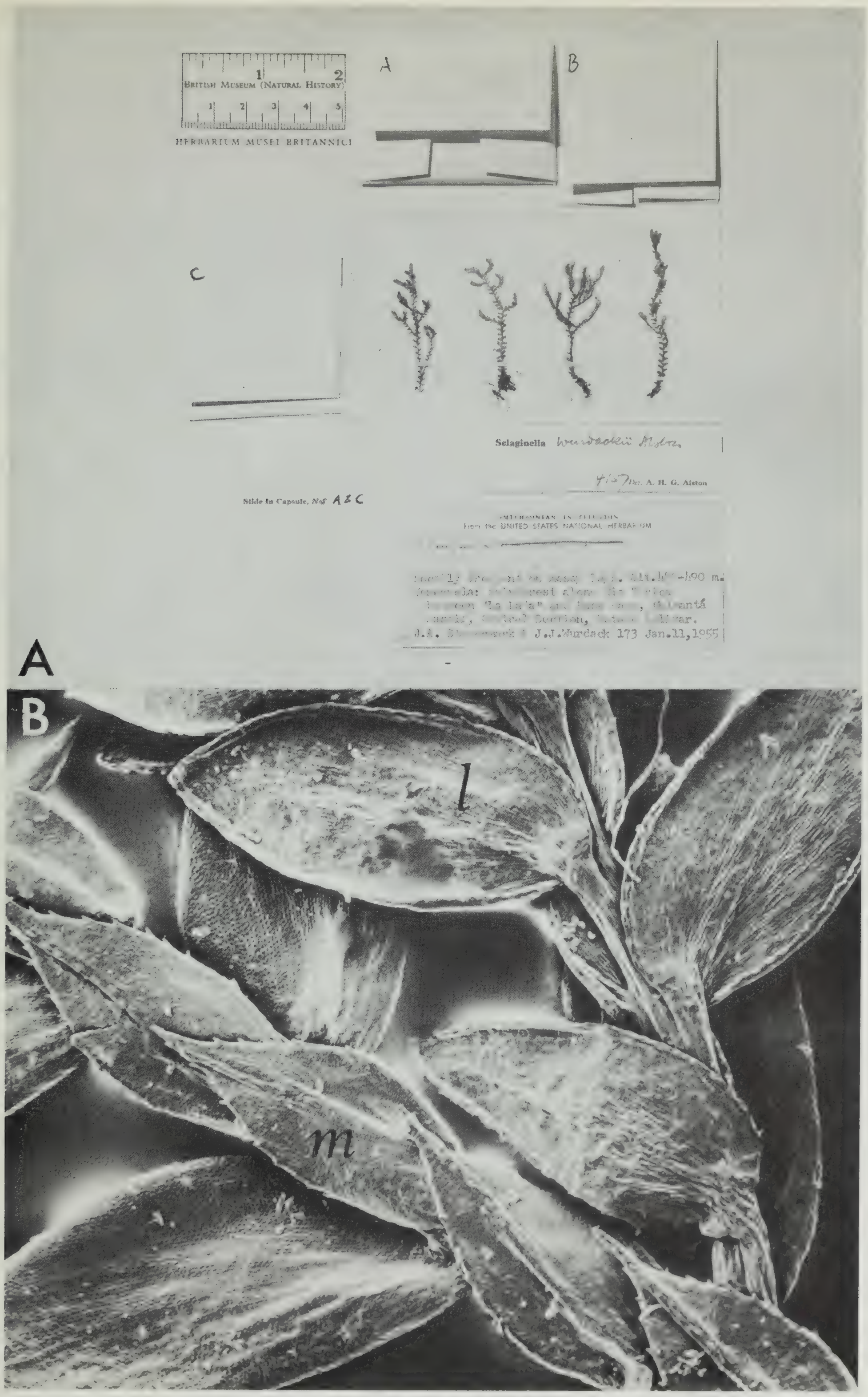

Fig. 9 *Selaginella wurdackii* Alston: **A.** Type specimen, *Steyermark & Wurdack* 173 (BM). **B.** Close-up of lateral (*l*) and median (*m*) leaves, × 33.

Notes: Baker gives the type locality as Panama, but the specimen is from the island of Cacagual, which is in Colombia.

64. Selaginella erectifolia Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 12 (1850); Baker, *Fern Allies* : 75 (1887). Type from Brazil, Rio de Janeiro, *Swainson* s.n. (K).
Selaginella camptostachys Fée, *Crypt. Brésil* : 299 (1869). Type from Brazil.
Selaginella glazioviana Hieron. in *Hedwigia* **43** : 36 (1904). Type from Brazil.

Specimens seen:
BRAZIL. Minas Gerais: Serra do Itacolumy, *Badini* 316 (BM). Rio de Janeiro: type as above; *Glaziou* 2242 (C, K, type of *S. camptostachys* Fée); Bocca do Matto (towards Nova Friburgo), 200—250 m, *Lutz* 1319 (BM). Santa Catarina; Fachina near Biguassu, *Rambo* 50378 (BM).

Geographical range: Confined to southern Brazil.

65. Selaginella roraimensis Baker in *Timehri,* **5** : 221 (1886), In *Trans. Linn. Soc. Lond.* (Bot.) II, **2** : 295 (1887), *Fern Allies* : 86 (1887). Type from Venezuela, Bolivar: Roraima, *im Thurn* 122 (BM).

Specimens seen:
GUYANA. Essequibo: Macouria Creek, Essequibo River, *Jenman* 2324 (BM) s.n. (NY).
VENEZUELA. Bolívar: near Mt Roraima, *Jenman* s.n. (NY); type as above.

Geographical range: Confined to the Roraima massif and west Guyana.

Notes: The specimens from Macouria Creek have slightly broader leaves and a more diffuse habit, but do not seem specifically separable. *S. porelloides* (No. 103) is a smaller species, with ovate lateral leaves and median leaves which are aristate or acuminate; *S. rhodostachya* (No. 86) has more ovate lateral leaves and a more creeping habit.

66. Selaginella scintillata Alston, **sp. nov.** (Figs 10 & 11)
Species heterophylla ex affinitate *S. roraimensis*, sed minus ramosa et foliis minoribus et rhizophoris brevibus filiformibus differt.

Planta ascendens; *caulibus* glabris, circa 7 cm altis, basi 0·75 mm in diam., e basi ramosis, rhizophoris ad tertiam partem basin versus restrictis; parte ramosa ambitu anguste elliptica, ramis *c.* 6 mm inter se distantibus, simplicibus vel irregulariter et distante pinnatis, plerumque *c.* 7 mm longis, sed usque ad 5 cm. *Folia* ubique heteromorpha; *folia lateralia* plusminusve patentia, contigua, leviter imbricata vel distantia, ovato-oblonga, 1·5 mm longa, fere 1 mm lata, subobtusa; semifacie superiore semi-ovata, basi rotundata, crebre serrata, apicem versus integra, aliter distante serrulata; semifacie inferiore semi-oblonga, basi vix cuneata, integra; *folia axillaria* lateralibus subsimilia; *folia intermedia* breviter ovato-oblonga, 1 mm longa, 0·8 mm lata, distante serrata, apice acuto, vix acuminato. *Strobili* in apicibus ramulorum lateralium singuli dispositi, tetragoni, *c.* 3·5 mm longi, 1·5 mm lati, non ramosi; *sporophylla* late ovata, leviter carinata, irregulariter serrulata, apice acuto; *megasporae c.* 300 μm, pallide brunneae (humectae), scabrae rugoso-reticulataeve; *microsporae c.* 30 μm, verruccatae, verrucis minute spinulosis.

Typus: Venezuela, Bolivar: Cana Mojado, Chimantá Massif, Toronotepui, 1895–1910 m, *Steyermark & Wurdack* 1079 (BM, holotype; US, isotype).

Other specimens seen:
VENEZUELA. Bolívar: vicinity of upper falls, Rio Tirica, Chimantá Massif, 1940—1950 m, *Steyermark & Wurdack* 536 (BM, US).

Geographical range: Confined to the Chimantá Massif, Venezuela.

67. Selaginella flexuosa Spring in *Flora, Jena* **21** : 197 (1838), in Martius, *Fl. Bras.* **1** (2) : 122 (1840), in *Bull. Acad. r. Belg.* **10** : 144 (1843). Syntypes from Brazil: without exact locality, *Swainson* s.n. (K); Corcovado, *Raddi* s.n. (BR?); around Rio de Janeiro, *Langsdorff* s.n. (BR?); Serra de Cubatao, *Guillemin* s.n. (?G). The latter three not seen.

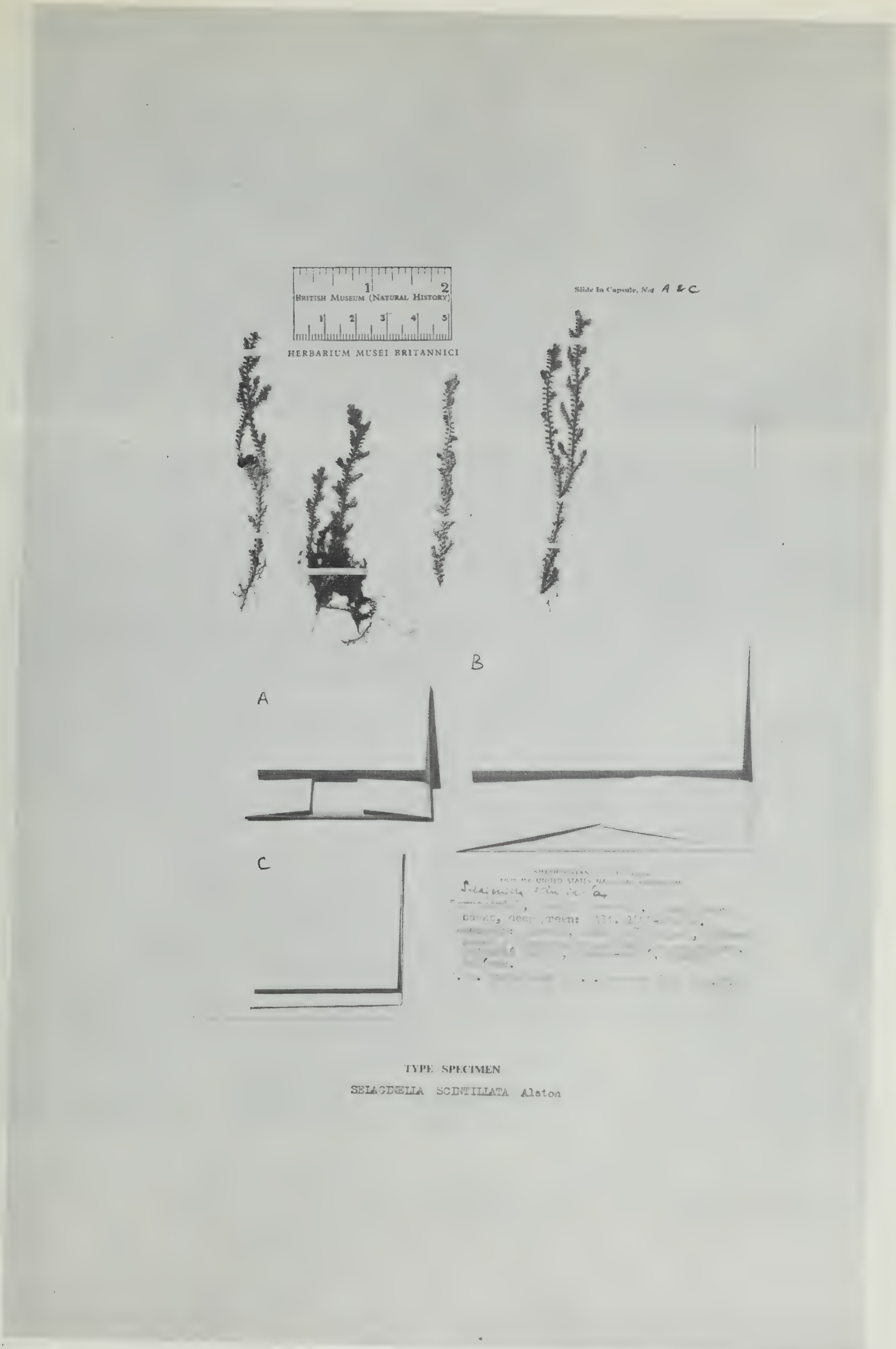

Fig. 10 *Selaginella scintillata* Alston: Type specimen, *Steyermark & Wurdack* 1079 (BM).

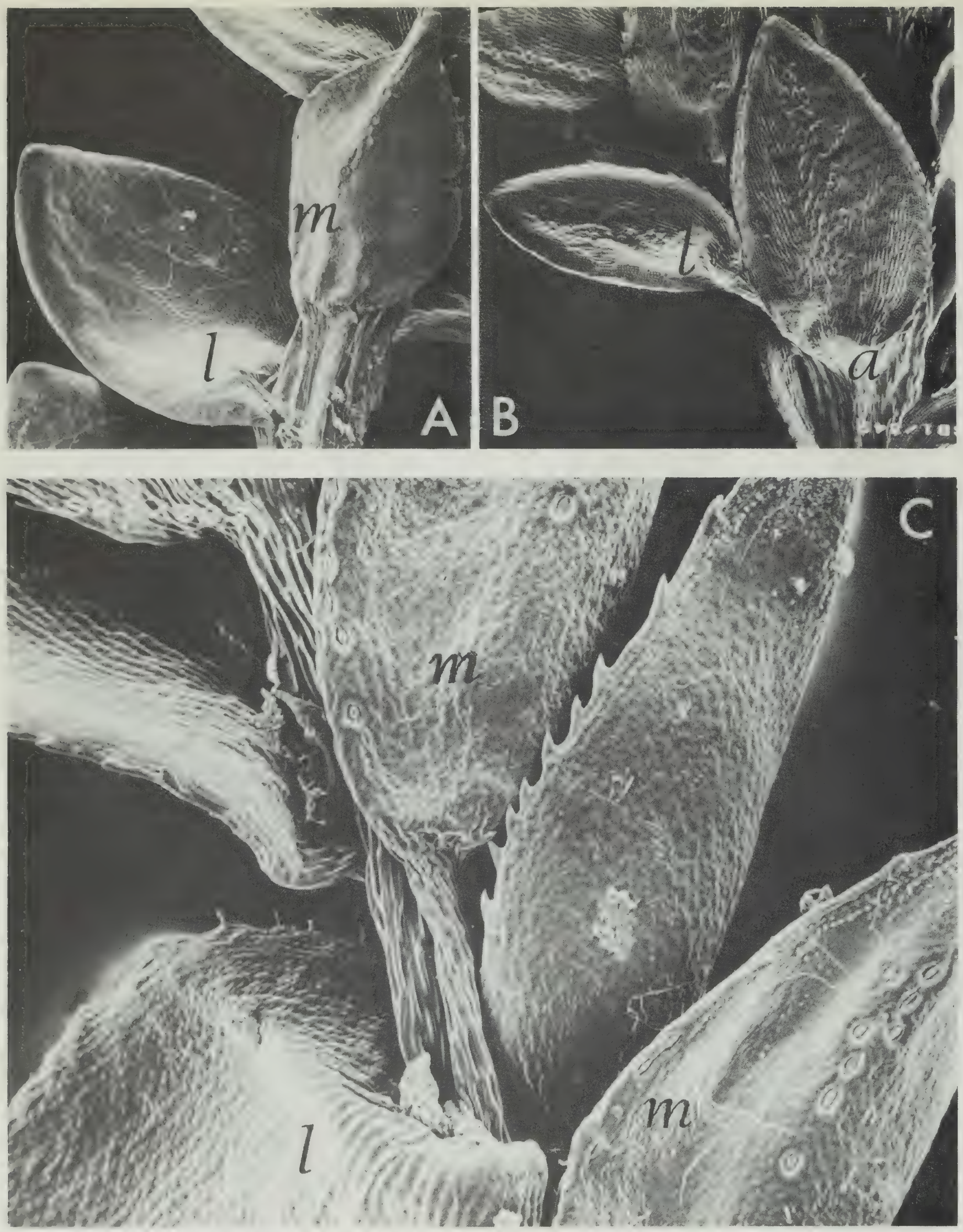

Fig. 11 *Selaginella scintillata* Alston: **A**. Close-up of lateral (*l*) and median (*m*) leaves, × 33. **B.** Close-up of lateral (*l*) and axillary (*a*) leaves, × 24. **C.** Median leaves (*m*) and axil of lateral leaf (*l*) showing ligule, × 108. All from *Steyermark & Wurdak* 1079.

Lycopodium brasiliense Desv. in *Mém. Soc. linn. Paris* **6** : 190 (1827), non Raddi (1825). Type from Brazil.

Selaginella brasiliensis (Desv.) Spring in *Flora, Jena* **21** : 213 (1838), non (Raddi) A. Braun (1865). Type as above.

Selaginella bella Fée, *Crypt. Bras.* **2** : 100 (1873); Hieron. in *Hedwigia* **43** : 4 (1903). Syntypes from Brazil.

Selaginella longicuspis Baker in *J. Bot., Lond.* **21** : 241 (1883). Type from Brazil.

Selaginella macrorhyza Silveira in *Bolm Comm. geogr. geol. Minas Geraes* **5** : 121 (1898); Hieron, in *Hedwigia* **43** : 37 (1904). Type from Brazil.

Selaginella brevipes sensu Baker, *Fern Allies* : 45 (1887), non Fée (1869) nec A. Braun (1867).

Specimens seen:

BRAZIL. Without exact locality: type as above; *Glaziou* 4491 (C, syntype of *S. bella* Fée), 4494 (C, syntype of *S. bella* Fée), 4504 (C, syntype of *S. bella* Fée, P), 4483 (C); *Bowie & Cunningham* s.n. (BM); *Capanema* s.n. (BM); *Dusul* 3720 (BM); *Riedel* s.n. (BM). Espirito Santo: Alto Limoeiro—Santa Maria, *Brade, Pereira & Duartz* 18276 (BM); Cachoeiro do Itapemirim, vargem Alta: Morro de Sul, *Brade* 19359 (BM); Castelo, Braco do sul, 800 m, *Brade* 19211 (BM), 19214 (BM), 19310 (BM). Minas Gerais: Conselheiro Matta, *Brade* 13963 (BM); Serra do Caraça, *Hoehne* s.n. (BM); near Rio Preto, *Silveira* 161 (BM); Ouro Preto, *de Godoy* 8420 (SP); *Damazio* 733 (P); S. Sebastian, *Damazio* 732 (P); *Silveira* 170 (P); Avraial de Bento Rodrigues, *Damazio* 1876 (P); Bello Horizonte, Serra da Mutuca, *Markgraf, Barreto & Brade* 3573 (BM); *Badini* 318 (BM); Sta. Barbara do Matto Dentro, *Hoehne* 5004A (BM); S. Sebastiãs de Paraiso, Cachoeira do Baú, *Brade & Pereira* 17954 (BM). Parana: Rio Branco, *Dusen* s.n. (BM); Palmeira, *Freitas* 57 (BM); Villa Velha, *Dusen* 14856 (C), 14906 (C); Ypiranga, *Dusen* 3720 (P). Rio de Janeiro: *Macgillivray* s.n. (BM), *Glaziou* 1645 (BM, C); Tijuca, *Friere* s.n. (BM); *Alston & Brade* 9012 (BM); *Glaziou* 7353 (BM, C, K, type of *S. longicuspis*); *Freire* 4 (BM); serra do Cariacica, *Brade* 13983 (BM); *Smith* 1273 (BM, C); *Brade* s.n. (BM); *Occhioni* 3 (BM); Petropolis—Casangola Morro do Muiz, *Goes & Constantino* 1032 (BM); Corcovado, *Peckolt & Freire* 481 (BM); Av. Niemeyer, *Pilger & Brade* s.n. (BM); Itatiaia, *Brade* 10059 (BM), 10236 (BM); 800 m, *Brade* 17221 (BM); 14529 (BM); Estrada Maromba, *Vaughan Bandeira* s.n. (BM); Morro Queimado, *Brade* 15722 (BM). Santa Catarina: Joinville, *Mueller* 133 (NY); *Mueller* s.n. (Rosenstock exsicc. 336; BM). São Paulo: Alto da Serra, *Usteri* 28a (BM, P); *Luederwaldt* 1658 (BM); *Gehrt* s.n. (BM); Santos, *Mosen* 3813 (C); Caroa da Muerte, Santos, *Schreiter* 12 (B).

Geographical range: Endemic to Brazil.

Notes: S. longicuspis Baker appears to differ only in size.

68. Selaginella decomposita Spring in Martius, *Fl. Bras.* **1** (2) : 123 (1841), *Bull. Acad. r. Belg.* **10** : 226 (1843). Syntypes from Brazil, Sebastianopolis, *Langsdorff* s.n. (?B), *Guillermin* s.n. (?BR).

Selaginella subsegregata Baker in *J. Bot., Lond.* **21** : 334 (1883), *Fern Allies* : 59 (1887). Type from Brazil.

Selaginella assurgens Baker in *J. Bot., Lond.* **22** : 277 (1884), *Fern Allies* : 78 (1887). Type from Brazil.

Selaginella fusca Silveira in *Bolm Comm. geogr. geol. Minas Geraes* **5** : 123 (1898). Type from Brazil.

Specimens seen:

BRAZIL. Without exact locality: *Glaziou* 7278 (C, P), 11722 (C, P), 4501 (C, type of *S. subsegregata* Baker), 7968 (C, syntype of *S. assurgens* Baker); *Burchell* 2238 (K, syntype of *S. assurgens* Baker). Ceará: Baturité, S. Joáo, *Leitz* 1360 (BM). Espirito Santo: Alto Limasiro, *Brade, Altaniro & Apparici* 18129 (BM); Castelo, Forno Grande 1000 m, *Brade* 19291 (BM); Cachociro do Iterpemirim, Vargem Alta, Morro de Sal, *Brade* 19360 (BM). Minas Gerais: Serra do Rio Preto, *Silveira* 162 (BM). Parana: Ypiranga, *Dusen* 8322 (BM); Lucena, *Wielewski* 71 (NY). Rio Grande do Sul: Serra do Estrella, 700 m, *Brade* 18657 (BM). Rio de Janeiro: *Glaziou* 5215 (C, K, syntype of *S. assurgens* Baker), 4501 (K), 5637 (C, K, P, syntype of *S. assurgens* Baker), 7768 (K); Itatiaia, *Brade* 10190 (BM), 10238 (BM); Maromba, *Brade* 14532 (BM); Petropolis 'Independencia', *Alston & Lutz* 273 (BM); Cachamba Road, Petropolis, *Glaziou* s.n. (BM, P); St Antonia de Finbé, *Brade & Luis* 11663 (BM); Serra dos Orgãos, *Gardner* 76 (K, syntype of *S. assurgens*); *Guillemin* 962 (P); Terezopolis, *Brade* s.n. (BM); Terezopolis, Cachoeira Teroz, *Lutz* 2087 (BM). Santa Catarina: Laranjeira mts, *Ule* 129 (P); Queimadas, *Spannagel* 196 (NY). São Paulo: *Usteri* s.n. (BM); Alto da Serra, *Luederwalt* 1656 (BM); *Gehrt* 4396 (BM); *Usteri*

25a (P), 21038 (P); Lorena, *Luederwaldt* s.n. (BM); Serra do Paranapiacaba, *Brade* 15716 (BM); Apiahy, *Schwacke* 2385 (P).

Geographical range: Endemic to Brazil.

Notes: S. subsegregata Baker and *S. assurgens* Baker are luxuriant specimens, *S. fusca* Silveira has rather more acute leaves than average *S. decomposita* but is still within the range of the species. It is closely allied to the West Indian *S. substipitata* Spring.

69. Selaginella duidae A. C. Smith in *Bull. Torrey bot. Club.* **58** : 312 (1931). Type from Venezuela, Bolivar: Laterite Valley, Savanna Hills, Duida, 1320 m, *Tate* 839 (NY, holotype; BM, isotype). The only specimen seen.

Geographical range: Confined to Mt Duida.

70. Selaginella euclimax Alston ex Crabbe & Jermy in *Fern Gaz.* **11** : 259 (1976). Type from Colombia, Cauca: W of Tambo, 2300 m, *Haught* 5220 (BM, holotype; COL, US, isotypes).

Specimens seen:
COLOMBIA. Antioquia: Rio Guapope, 15–1800 m, *Kalbreyer* 1457 (B, BM). Cauca: type as above.

Geographical range: Confined to Colombia.

Notes: This species resembles *S. tarapotensis* (No. 99), which is prostrate rather than erect, and has a longer arista on the median leaves. *S. pearcei* (No. 34) is also very similar, but it has broader lateral leaves with acute apices, very short aristae, and is usually less branched below. On the herbarium label in BM of *Kalbreyer* 1457 the altitude is given as 5–6000 metres, which cannot be the case; the error was perpetuated in Crabbe & Jermy (1976).

71. Selaginella vernicosa Baker in Timehri **5** : 220 (1886), in *Trans. Linn. Soc. Lond.* (Bot.) **52** : 295 (1887), *Fern Allies* : 78 (1887). Type from Venezuela, Bolivar: SE slopes of Mt Roraima, 'Our House', 1622 m, *im Thurn* 266 (K, US).
Selaginella vernicosa var. *oligoclada* Baker in *Trans. Linn. Soc. Lond.* (Bot.) **2** : 295 (1887), *Fern Allies* : 78 (1887). Type from Venezuela.
Selaginella vernicosa var. *simplicifrons* Jenman, *Ferns & Fern Allies W. Indies* : 401 (1908), in synonymy.

Specimens seen:
VENEZUELA. Bolívar: type, as above; Mt Roraima, summit, 2700—2740 m, *McConnell & Quelch* 574 (BM, NY); *Tate* 416 (BM, NY); *Steyermark* 57796 (US), 58016 bis & ter (US), 58889 (BM); SE slopes 'Our House' 1622 m, *im Thurm* 381 (BM, type of *S. vernicosa* var. *oligoclada* Baker); above Rondon Camp, 2070 m, *Tate* 466 p.p. (NY); Chimanta Massif, Central section, 1940 m, *Steyermark & Wurdack* 404 (BM).

Geographical range: Confined to La Gran Sabana.

72. Selaginella vestiens Baker in *J. Bot., Lond.* **21** : 97 (1883), *Fern Allies* : 43 (1887). Type from Brazil, Goias: Morro de Canto Gallo, *Burchell* 7006 (K).
Selaginella cladostachya Baker in *J. Bot., Lond.* **21** : 97 (1883). Type as above.
Selaginella erythrospora Silveira in *Com. Geogr. Geol. Est. Minas Geraes* **5** : 126 (1898). Type from Brazil.

Specimens seen:
BRAZIL. Bahia: Serra Sincora, 1400 m, *Ule* 7298 (BM). Goias: type, as above. Minas Gerais: *St Hilaire* 913 (P); Serro da Cipo, *Silveira* 156 (BM, type of *S. erythrospora* A. Silveira); Strada Pila, *Barret* 581 *& Brade* 144404 (BM); near Aguas Santas, Serra de S. José, *Silveira* 2622 (P); Campos de S. Sebasiao, *Damazio* 1882 (BM, P); Christias, near Corriga dois Puntes, Diamantina, *Mexia* 5832 (BM);

Serra do Rio Grande, 1260 m, Diamantina, *Mexia* 5799a (BM); Consulheiro Matta, *Brade* 13962 (BM). Rio de Janeiro: Morro de Cubicado, Petropolis, *Glaziou* 11723 (BM, C, P).

Geographical range: Confined to south-east Brazil.

Notes: Selaginella cladostachya was described by Baker at the same time as *S. vestiens* and from the same gathering made by Burchell. The variation in leaf length, width and shape of apex, and degree of density of cilia varies within the range of the species, and in our opinion these two entities cannot be distinguished.

73. Selaginella anisoclada Alston ex Crabbe & Jermy in *Fern Gaz.* **11** : 255 (1976). Type from Venezuela, Aragua: above Guamitas Parcque Nacional, 900 m, *Alston* 5814 (BM).

Specimens seen:
VENEZUELA. Aragua: type as above.
COLOMBIA. Magdalena: Sierra del Libano, Santa Marta, 1650 m, *Smith* 2242 (BM, NY, US); Santa Marta, *Smith* 2567 p.p. (BM).

Geographical range: Confined to the coastal ranges of Venezuela and Colombia.

Notes: The species is distinct in its distant arrangement of both median and lateral leaves, which are almost isomorphic on the ultimate branches. It varies in stature of plant and degree of branching, a character obviously affected by the moistness of, and competition in, the habitat. It is most similar to *S. porphyrospora* (No. 44), but there the lateral leaves are larger, lanceolate and acute. *S. lychnuchus* (No. 47) can be similar in habit, but that species has dimorphic sporophylls and large, oblong, lateral leaves, and long, aristate, median leaves.

74. Selaginella microphylla (Kunth) Spring in *Bull. Acad. r. Belg.* **10** : 234 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 88 (1850); Baker, *Fern Allies* : 41 (1887), p.p. excl. pl. guatemalensis. Type from Colombia, Cauca: Qulcacé, *Bonpland* s.n. (BM).
Lycopodium microphyllum Kunth, *Nov. Gen. Spec.* **1** : 37 (1816), *Syn. Pl. Itin. Orb. Nov. Humb. Bonpl.* : 96 (1822); Spreng, *Syst. Veg.* **4** : 15 (1827). Type as above.
Selaginella thujaefolia Spring in Martius, *Fl. Bras.* **1**, pt 2 : 120 (1840), in *Bull. Acad. r. Belg.*, **10** : 140 (1843). Type from Uruguay.
Selaginella jamesoni Baker in *J. Bot., Lond.* **21** : 97 (1883), *Fern Allies* : 42 (1887). Syntypes from Ecuador.
Selaginella microphylla f. *communis* Sodiro, *Rec. Crypt. Vasc. Quito* : 92 (1883), nom. nud.
Selaginella microphylla f. *culcitrella* Sodiro, *Rec. Crypt. Vasc. Quito* : 92 (1883). Type from Ecuador.
Selaginella schmidtchenii Hieron. in *Hedwigia* **43** : 40 (1904). Type from Colombia.

Specimens seen:
VENEZUELA. Merida: *Moritz* 369 (BM); Merida, 1800 m, *Alston* 6703 (BM).
COLOMBIA. Without precise locality: *Schmidtchen* s.n. (B, type of *S. schmidtchenii* Hieron.; BM). Antioquia: near Antioquia, 550 m, *Barkley, Klevens & Gutiérrez* 17c377 (BM, COL). Cauca: Qulcacé, 104 hexap., *Bonpland* s.n. (BM, type collection of *Lycopodium microphyllum*). Cundinamarca: Choachi, 1800 m, *Lindig* 1519 (BM); Camino de Villavicencio, *Dawe* 273 (US). Huila: 3 km SE of Neiva, 510 m, *Little* 9475 (COL); 6 km N of Neiva, 450 m, *Little* 8945 (COL). Nariño: Rio Guaitara, 1500 m, *Lehmann* 777 (NY); Pasto, 2500 m, *Espinosa* 2750 (BM). Tolima: Chicoral, 450 m, *Haught* 6386 (BM, COL); Gualandaya, between Espinal and Ibagué, 700 m, *Alston* 7704 (BM).
ECUADOR. Without precise locality: *Spruce* 4787 (BM, CGE, NY). Azuay: near Cuenca, *Rose* 22869 (NY, US). Chimborazo: Cañon of Rio Chanchan near Huigra, 1200–1350 m *Camp* E 3205 (BM); near Huigra, *Rose* 23959 (NY); Chambo, 2800 m, *Asplund* 5952 (S). Pichincha: *Jameson* 280 (BM); Machbnagara, *Sodiro* 30 (NY); near Quito, *Couthouy* 84 (NY), 2850 m, *Mille* s.n. (NY); below Guápulo, near Quito, 2500 m, *Asplund* 6708 (S); Chaupi-sagcha, Pululagua, 1800 m *Bell* 444 (BM); Panecillo, Quito, 2900 m, *Asplund* 6071 (S). Santiago-Zamora: Tambo Chontal to Tambo Consuelo, 1710–2400 m *Camp* E 1586 (BM). Tungurahua: Baños, 1400 m, *Asplund* 19904 (S).

PERU. Without precise locality: *Mathews* s.n. (BM, NY). Cuzco: San Miguel, Urubamba valley, 1800 m, *Cook & Gilbert* 1782 (US); Quellounu, 950 m, *Buez* s.n. (B).
BOLIVIA. Without precise locality: *Rusby* 2117 (NY). Cochabamba : Cochabamba, *Bang* 1097 (BM, NY); Sailapata, Ayopaya, 2700 m, *Cardenas* 3234 (BM); on rock, lomo de San Pedro, Botanic Garden 2520 m, *Hermann* 24600 (BM). La Paz: Sorata, Larecaja, 2250 m, *Williams* 1404 (NY); 2400 m, *Rusby* 456 (NY); Yungas, *Jay* (NY), a[bis]d (NY); Sorata (E of L Titicaca), 2400 m, *Brooke* 6649 (BM). Santa Cruz: Cortés, 1800 m, *Williams* 1403 (NY); Cerro La Negra, 1800 m, *Steinbach* 8186 (NY); Cerro Tres Cruzas, 1500 m, *Steinbach* 8165 (NY).
BRAZIL. Without exactly locality: *Glaziou* 7967 (C). Minas Gerais: Caldas, *Mosen* 2025 (BM, NY, P). Rio Grande do Sul : Antonio Prado, *Dutra* 116 (BM); Rio Pardo, Fazenda Leitão, *Jurgens* L7 (BM, NY); Böhmerbach, *Jurgens* L28 (BM, NY). Sao Paulo: Serra de Botucatu, *Hoehne & Gehrt* 33529 (BM); campos do Jordão, *Porto* 3113 (BM); Pedra do Baú, São Bento do sa pucai, 1900 m, *Leitz* 3929 (BM). Santa Catarina: Serra do Oratorio, *Ule* 297 (BM, P); Braço serafim, Itajaí, 200 m, *Reitz* 3016 (BM).

Geographical range: From Venezuela along the Andes to Argentina, and east to southern Brazil, Paraguay and Uruguay.

Notes: Selaginella schmidtchenii was described from an abnormal specimen with no further data than 'Nova Granada, 1882'; in our opinion it is a form of *S. microphylla*; the curling up of the lateral leaves might be caused by drought or frost. Similar specimens have been collected elsewhere in Colombia by *Haught* 6386 (BM) and *Alston* 7704 (BM).

75. Selaginella schultesii Alston ex Crabbe & Jermy in *Am. Fern J.* **63** : 141 (1973). Type from Colombia, Amazonas: Rio Popayaca, tributary of R. Apaporis, *Schultes & Cabrera* 15561 (US, holotype; BM, isotype).

Specimens seen:
COLOMBIA. Amazonas: type as above; Raudal Yayacopi, La Playa, 240 m, *Schultes & Cabrera* 15417 (US), 16205 (US), 16898 (BM, US). Vaupés: Cachoiera Miriti, Rio Kanari, 250 m, *Schultes & Cabrera* 14411 (COL, US); Cerro Isibukuri, Rio Kananari, 250–700 m, *Schultes & Cabrera* 13314 (COL, US); Rio Apaporis, Cachivera de Jirijirimo y alrededores, 250 m, *Schultes & Cabrera* 12456 (COL, US); Rio Apaporis, Raudal de Jirijirimo 270 m, *Schultes & Cabrera* 14554 (COL), 14598 (COL).

Geographical range: Confined to Colombia.

Notes: Schultes notes (in sched.) that this plant is known to the Makuna Indians as 'wee-wee-a-ree' suggesting that it may have had a local use. *S. homaliae* (No. 95) is similar in habit, but has more oblong lateral leaves, usually twice as long as broad, which are rounded at the apex and almost without cilia. *S. applanata* (No. 98) is again similar, but has more elongated and even larger leaves (up to 2·5 mm).

76. Selaginella microdonta A. C. Smith in *Bull. Torrey bot. Club* **58** : 313 (1931). Type from Venezuela, Amazonas: on slope of Ridge 24 and summit of Mt Duida, 1800 m, *Tate* 509 (NY, holotype; BM, isotype).

Specimens seen:
VENEZUELA. Amazonas: types as above. Bolivar: Ptari-teoui, 2885–2405 m, *Steyermark* 59563 (BM, US).

Geographical range: Mountains of southern Venezuela.

Notes: This species resembles *S. rotundifolia* Spring of the West Indies, but the median leaves are narrower and more acuminate. *S. ovifolia* subsp. *philipsonii* (No. 83) differs in having distinctly ciliate lateral leaves.

77. Selaginella jungermannioides (Gaudich.) Spring in *Bull. Acad. r. Belg.* **10** : 143 (1843); Baker, *Fern Allies* : 53 (1877) Type from Brazil, Rio de Janeiro, *Gaudichaud* s.n. (K).

Lycopodium jungermannioides Gaudich. in Freyc., *Voyage Autour Monde, Bot.* 286 ['826'] (1828). Type as above.

Lycopodium marginatum sensu Raddi, *Pl. Bras. Nov. Gen.* : 82 (1825), excl. syn.

Specimens seen:

BRAZIL. Without exact locality: *Glaziou* 4675 (C), 7493 (C), 7965 (C, P), 12295 (C). Espirito Santo: Rio Mutuni, *Luetzelburg* 9942 (M). Rio de Janeiro: type as above; *Raddi* s.n. (BM); *Mosen* s.n. (M); Tijucca, *Usteri* s.n. (BM); *Alston & Brade* 9004 (BM); *Brade* 10031 (BM); Corcovado, *Rudio* s.n. (BM); *Luetzelburg* 9960 (M); Serra Estrella, *Luetzelburg* 7386 (M), 7875 (M); Serra dos Orgãos, *Luetzelburg* 7045 (M); Ilha Grande, *Rose & Russell* 20349 (NY); St Antonio de Finba, *Brade & Luis* 11672 (BM).

Geographical range: Confined to eastern Brazil.

78. Selaginella arenaria Baker in *J. Bot., Lond.* **21** : 82 (1883), *Fern Allies* : 40 (1887); Alston in *Reprium Spec. nov. Regni veg.* **40** : 317 (1936), p.p. quoad spec. typic. Type from Brazil, Amazonas: On Rio Vaupes at Panuré, *Spruce* 2861 (K). The only collection.

Geographical range: West Brazil.

Notes: There is a note on the type sheet at K, in what appears to be Spruce's handwriting, stating: 'I believe some barren specimens of this were mixed up with No. 2535; the two are however quite distinct.' Specimens under this collecting number have been distributed to several herbaria; but so far the type is unique and the other specimens do not match any hitherto described species. They are described as *S. calceolata* (No. 118, p. 314).

79. Selaginella brevifolia Baker in *J. Bot., Lond.* **21** : 83 (1883), *Fern Allies* : 41 (1887). Alston in *Reprium Spec. nov. Regni veg.* **40** : 312 (1936). Type from Brazil: *Spruce* 2547 (BM, CGE, K).

Selaginella cryptogaea Baker in *J. Bot., Lond.* **21** : 98 (1883), *Fern Allies* : 44 (1887). Type from Brazil, Amazonas: on rocks by the Janaraté Cachoeira, near Panure, *Spruce* 2547 (K holotype; BM, CGE, isotypes).

Specimens seen:

VENEZUELA. Amazonas: Rios Pacimoni-Yatua, Casiquiare, 110–130 m, *Maguire, Wurdack & Bunting* 37468 (BM). Bolivar: Salto de Para, Medio Caura, 300 m, *Williams* 11385 (BM).

COLOMBIA. Huila: 1 km east of Neiva, 510 m, *Little* 9250 (COL). Vaupés: Rio Vaupés, 75 m, *Schultes & Cabrera* 13866 (BM); Cerro de Tipiaca, between Mitu and Javarete, *Schultes & Cabrera* 19319 (US); Cerro Yapoboda, Rio Kuduyari, 450 m, *Schultes & Cabrera* 14182 (COL, US), 14215 (COL, US).

PERU. San Martin: Boqueron between Tingo Maria and Pucallpa 400 m, *Allard* 22124 (BM).

BRAZIL. Amazonas: type, as above; near San Gabriel da Cachoeira, Rio Negro, *Spruce* 2328 (BM, CGE); *Schultes & Lopez* 9171 (BM); Piedra de Cocui, Rio Negro, *Schultes & Lopez* 9428 (BM); San Felipe, *Luetzelburg* 22129 (M); Serra Wabeesee, below Bela Vista, Rio Uaupés, *Schultes & Pires* 9147 (BM); near Panure, Rio Uaupés, *Spruce* 2905 (BM, K, type of *S. cryptogaea* Baker).

Geographcal range: Venezuela, Colombia, Peru and the western part of Brazilian Amazonas.

Notes: This species is very closely allied to *S. cordifolia* (Desv.) Spring from Cuba, Hispaniola and Porto Rico, but that species has longer, aristate, median leaves and is often flagelliferous. *S. muscosa* (No. 88) may be confused with some forms of *S. brevifolia*, but the lateral leaves are denticulate and the median leaves have longer aristae. *Maguire, Wurdack & Bunting* 37468 has distinct almost triangular leaves on the main stem. *Allard* 22124 is a sterile specimen with median leaves that have oblique bases with an auricle on the outer side; it is close to this species but may be found not to be conspecific when more material has been studied.

80. Selaginella sandwithii Alston, **sp. nov.** (Figs 12 & 13)

Species heterophylla ex affinitate *S. deltoidei* sed habitu erecto et rhizophoris ad basin limitatis differt.

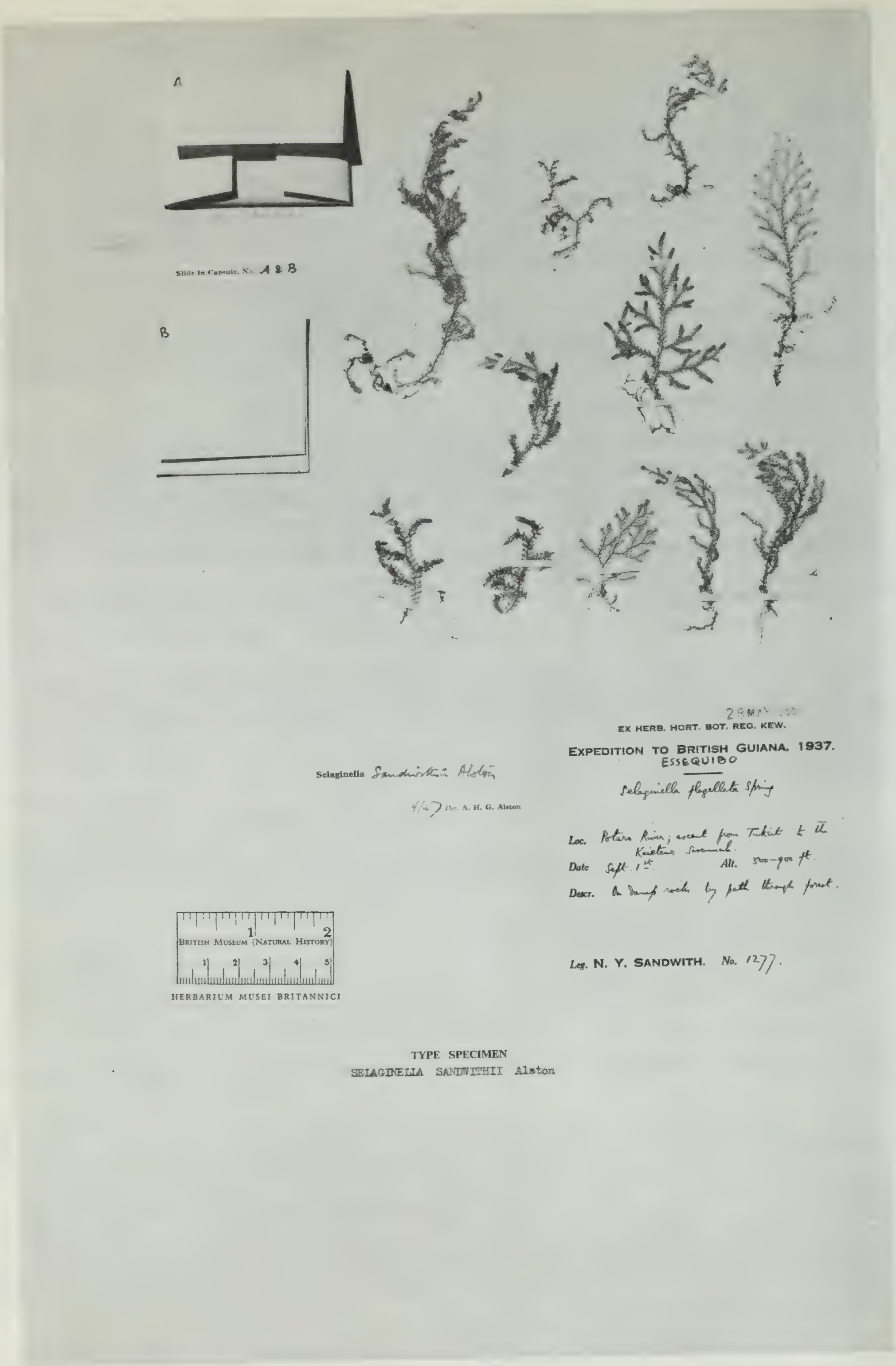

Fig. 12 *Selaginella sandwithii* Alston: Type specimen, *Sandwith* 1277 (BM).

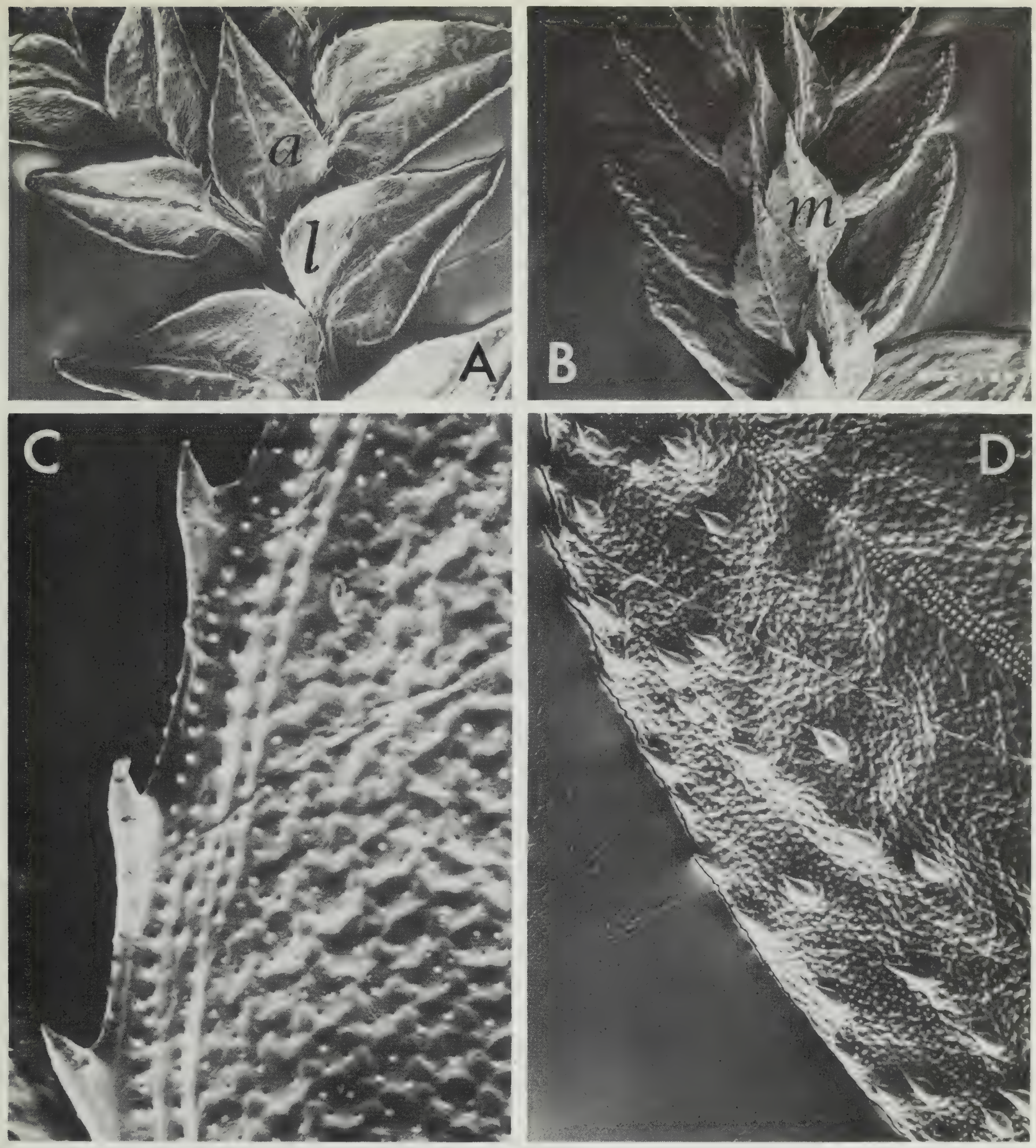

Fig. 13 *Selaginella sandwithii* Alston: **A.** Close-up of lateral (*l*) and axillary (*a*) leaves, × 15. **B.** Close-up of median (*m*) and lateral leaves; note laminal teeth (unicellular papillae) on upper surface of lateral leaves; × 22. **C.** Median leaf, lower surface, × 460. **D.** Lateral leaf, upper epidermis with unicellular papillae, × 143. All from *Sandwith* 1277.

Planta e basi repente ascendens vel erecta; *caulibus* glabris, 6–14 cm altis, basi 1 mm in diametro, e basi ramosis vel parte simplici usque ad 10 cm longa; rhizophoris ad tertiam partem basin versus restrictis; parte ramosa ambitu plerumque irregulariter ovata, ramis *c.* 1 cm inter se distantibus, pinnatis ambitu auguste ellipticis, usque ad 2·5 cm longis. *Folia* heteromorpha vel in parte simplici basin versus subaequalia; *folia lateralia* oblique patentia, crebre disposita vel leviter imbricata, ovato-deltoidea 2 mm longa, 1·25 mm lata, acuta; in epidermide superiore marginem versus papillis unicellularis praedita; semifacie superiore semi-ovatodeltoidea, basi rotundato-cordata breviter serrulato-ciliolata distanter minutissimeque serrulata, aliter integra; semifacie inferiore semi-oblongo-deltoidea, basi truncata, apice cuneato et distanter minutissimeque serrulato, alibi integra; *folia axillaria* ovato-

deltoidea, quam folia lateralia paullo minoria; *folia intermedia* ovata, *c.* 1 mm longa, 0·7 mm lata, serrata, valde albo-marginata basi leviter inaequilateralia, apice acuminato-aristato; arista dimidio breviore lamina. *Strobili* ad apicibus ramulorum omnium singulariter dispositi, subtetragoni, 3 mm longi, 1·5 mm lati, non ramosi; *sporophylla* anguste ovata, carinata, albomarginata, serrata, acuminata; *megasporae* non visae; *microsporae c.* 37 μm luteae (humectae) verrucosae verrucis minute spinulosis.

Typus: Guyana: Essequibo, Potaro River, ascent from Tukeit to Kaieteur savannah, 150–270 m, *Sandwith* 1277 (BM, holotype; K, isotype).

Other specimens seen:
SURINAM. Saramacca: Tafelberg, *Maguire* 24336 (BM, NY), 24553 (BM, NY), 24772 (BM, NY).
GUYANA. Essequibo: Kaieteur gorge, *Tutin* 536 (BM); *Sandwith* 1501 (BM); Kaieteur Plateau, *Maguire & Fanshawe* 23416 (BM).

Geographical range: Sandstone area of Surinam and Guyana.

Notes: Alston was long puzzled by this species and referred some specimens to *S. flagellata* (No. 41) and others to *S. muscosa* (No. 88). The former differs by its flagelliform apices and microspores with elongate papillae; the latter by its prostrate habit. *S. brevifolia* (No. 79) is also similar, but differs by its ciliate lateral leaves. We are retaining this as a new taxon with the belief that, as more material becomes available, it may be merged with *S. deltoides* A. Braun, a segregate of *S. muscosa* (see notes on p. 298).

81. Selaginella valdepilosa Baker in *J. Bot., Lond.* **21** : 82 (1883), *Fern Allies* : 40 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 250 (1950). Type from Guyana: Essequibo: ravines near the Kaieteur Savannah, *Jenman* 1484 (K, holotype; BM, NY, isotypes).
Two subspecies are distinguished:

subsp. **valdepilosa.**

Specimens seen:
GUYANA. Essequibo: type as above; on precipices of Kaieteur Gorge. 360 m, *Sandwith* 1435 (BM, K); Waratula, Potaro R., *Tutin* 480 (BM); *Maguire & Fanshawe* 23415 (BM).

Geographical range: Confined to Guyana.

Notes: Two specimens in BM (Brazil: Rio Grande do Sul: Montenegro, S. Salvador, *Sehnem* s.n. [Hb *Dutra* 1233]) are very near this species morphologically, but need further investigation.

subsp. **tricholoma** Jermy & Rankin, **subsp. nov.** (Fig. 14)
Planta subsp. *valdepilosae* similis sed foliis angustioribus, plerumque inter se distantibus differt.

Planta omnino repens prostrataque; *caulibus* glabris, flexuosis, subfiliformibus, in siccitate pallide stramineis, *c.* 12 cm longis, distanter alternatim pinnatis nonnunquam bipinnatis, rhizophora ubique gerentibus; ramis *c.* 10 mm inter se distantibus, usque ad 25 mm longis, furcatis. *Folia* ubique heteromorpha; *folia lateralia* patentia, paullum distantia vel subcontigua, elliptico-oblonga, 1 mm longa, 0·75 mm lata, obtusa, fere aequilateralia, utrinque ciliata; semifacie superiore late semi-elliptico-oblonga; semifacie inferiore semi-elliptico-oblonga; *folia axillaria* aequilateralia; *folia intermedia* elliptico-orbiculata, basi rotundata, 0·7 mm longa, 0·60 mm lata, apice obtusa, ubique ciliata, oblique patentia; *strobili* non visi.

Typus: Guyana: Essequibo: vertice montis Roraima, 2700–2740 m, *Steyermark* 58016 (BM, holotype; US isotype).

Geographical range: Known only from the type collections from Mt Roraima.

Notes: This species also resembles *S. rhodostachya* (No. 86), which has more ovate lateral leaves. Material under the type number, labelled 58016 bis (BM, US) is a mixture of this

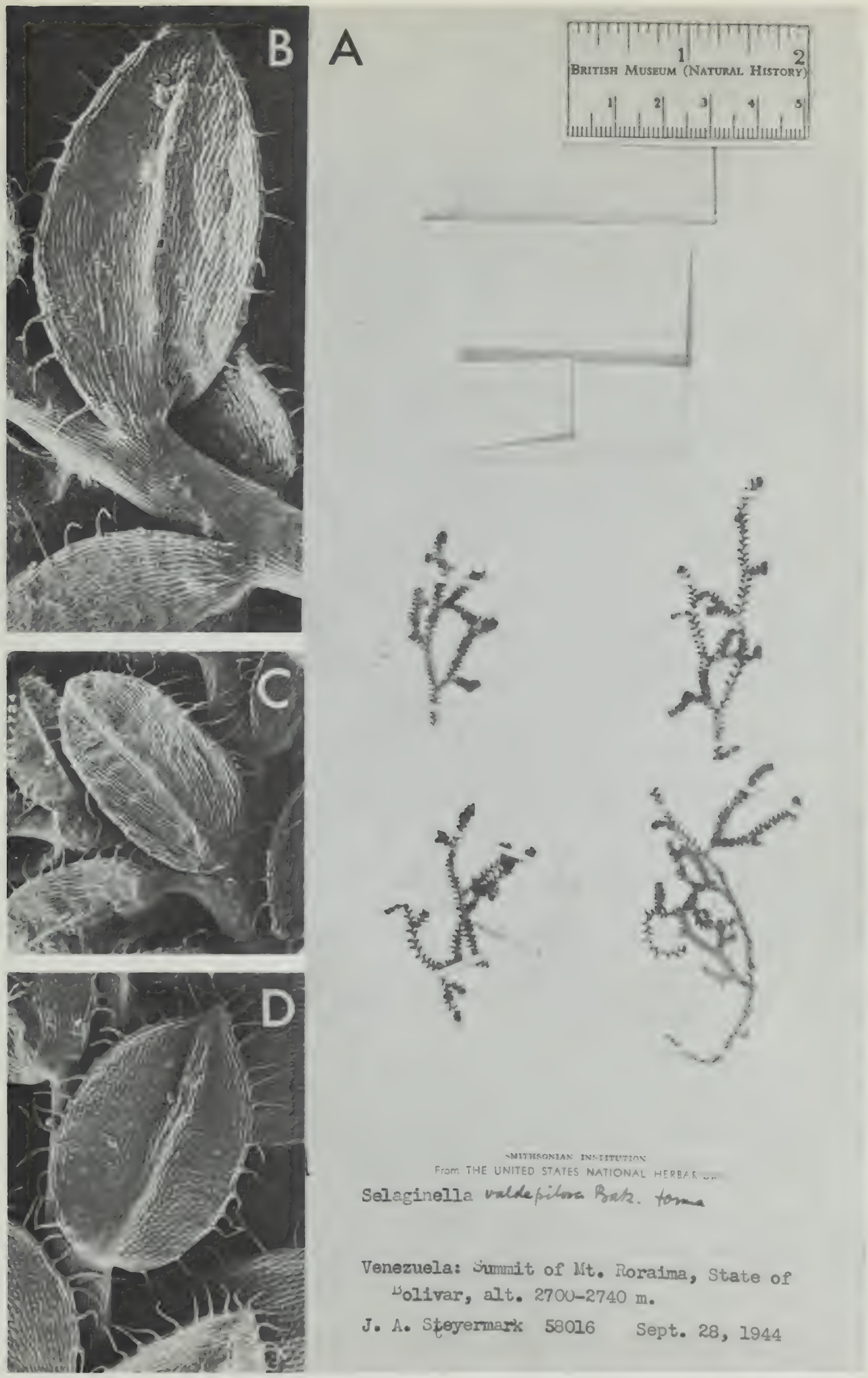

Fig. 14 *Selaginella valdepilosa* subsp. *tricholoma* Jermy & Rankin: **A.** Type specimen, *Steyermark* 58016 (BM). **B.** Close-up of lateral leaf, × 40. **C.** Close-up of axillary leaf, × 25. **D.** Close-up of median leaves, × 40.

subspecies and *S. vernicosa* (No. 71), and is best treated as a paratype. Alston was inclined to treat this taxon as a species; we feel it is very close to *S. valdepilosa* s.str. and at the moment prefer to give it subspecific rank, but as more material is collected it may even prove to be a growth form of that species.

82. Selaginella fragillima Silveira in *Bolm Comm. geogr. geol. Minas Geraes* **5** : 127 (1898); Hieron. in *Hedwigia* **43** : 12 (1903). Type from Brazil: Serra de S. José d'El-Rei, *Silveira* 2622 (Herb. Com. Geog. e Geolog. Civitatis Minas Geraes).

Specimens seen:
BRAZIL. Minas Gerais: type, as above; S. Sebasitas de Paraiso, *Pereira, Brade & Barbosa* 17953 (BM); Serra do Lenheiro, *Silveira* 149 (BM).

Geographical range: Endemic to Brazil.

83. Selaginella ovifolia Baker in *J. Bot., Lond.* **2** : 90 (1884), *Fern Allies* : 68 (1887); Alston in *Bull. Br. Mus. nat. Hist.* (Bot.) **1** : 45 (1952) & 244 (1955). Type from Puerto Rico, *Schwanecke* s.n. (K).

Subsp. **philipsonii** Jermy & Rankin, **subsp. nov.** (Figs 15 & 16)
Subspecies a subsp. *ovifolia* foliis lateralibus minus acutis, longe ciliatis, foliis intermediis majoribus oblongioribusque differt.

Planta omino repens et prostrata; *caulibus* glabris, filiformibus, pallide luteo-viridis, 12 cm longis, distanter alternatim pinnatis, nonnunquam bipinnatis; rhizophora ubique gerentibus; ramis *c.* 1 cm inter se distantibus, usque ad 2 cm longis. *Folia* ubique heteromorpha; *folia lateralia* patentia, distantia, ovato-rotundata, 1 mm longa 0·75 mm lata, obtusa, fere aequilateralia; semifacie superiore, longe ciliata fere ad apicem; semifacie inferiore, basi integra, et apicem versus serrata; *folia axillaria* similia lateralibus; *folia intermedia* oblongo-elliptica, distantia, latere exteriore integra, basi rotundata et latere interiore serrata, basi cuneata, 0·6 mm longa, 0·45 mm lata, apice subacuto. *Strobili* non visi.

Typus: Colombia, Meta/Vaupés: Rio Guapaya, Macarena, 450 m, *Philipson, Idrobo & Fernandez* 1607a (BM, holotype).

Other specimens seen:
COLOMBIA. Meta: Margen del Rio Guayabero, 10 km abajo de Cano Lozada, 350 m, *Pinto & Bischler* 239 (COL); Sierra La Macarena, 'Cano Veinte', 500 m, *Idrobo* 4837 (BM). Norte de Santander: Catatumbo, Campo Oru y alrededores, 350–500 m, *Bischler* 2397 (COL); Catatumbo, Campo Tibu, 200 m, *Bischler* 2493 (COL).

Geographical range: confined to the Macarena Mts, Colombia. Subsp. *ovifolia* occurs in Central America and the West Indies.

Note: Alston treated this as a new species, but its similarity and presumed affinity to *S. ovifolia* Baker is so great that we have designated it as a subspecies of that species. It has lateral leaves which are obtuse with occasionally a mucronate apex, and median leaves which are less ciliate and more oblong than in the type subspecies. The specimens are sterile but we have confidence in designating it as a new taxon.

84. Selaginella cabrerensis Hieron. in *Hedwigia* **43** : 29 (1904). Type from Colombia, Tolima: Rio Cabrerea, near Colombia, 500–1000 m, *Lehmann* 6406 (K, US).
Selaginella daguensis Hieron. in *Hedwigia* **43** : 49 (1904). Type from Colombia.

Specimens seen:
COLOMBIA. Cundinamarca: Pandi, 900 m, *André* 1817 (BM, NY). Meta: Serra de la Macarena, 900 m, *Philipson* 2388 (BM). Tolima: type as above; Chichoral, 450 m, *Haught* 6333 (BM), 6439 (BM, COL). Valle de Cauca: Rio Dagua near Buenaventura, 0–300 m, *Lehmann* 4462 (K, type collection of *S. daguensis* Hieron.).

Geographical range: Confined to Colombia.

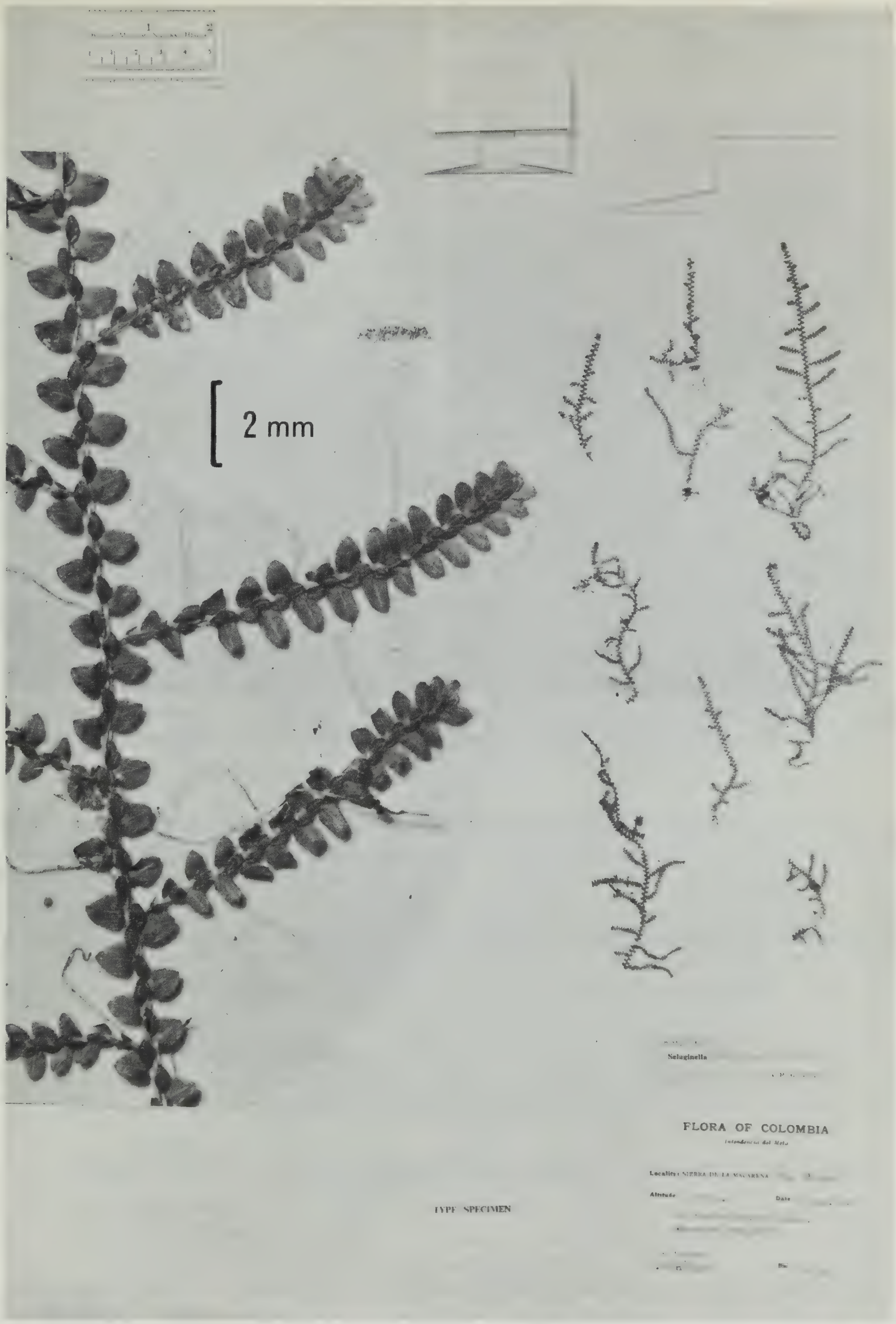

Fig. 15 *Selaginella ovifolia* subsp. *philipsonii* Jermy & Rankin: Type specimen, *Philipson, Idrobo and Fernandez* 1607a (BM).

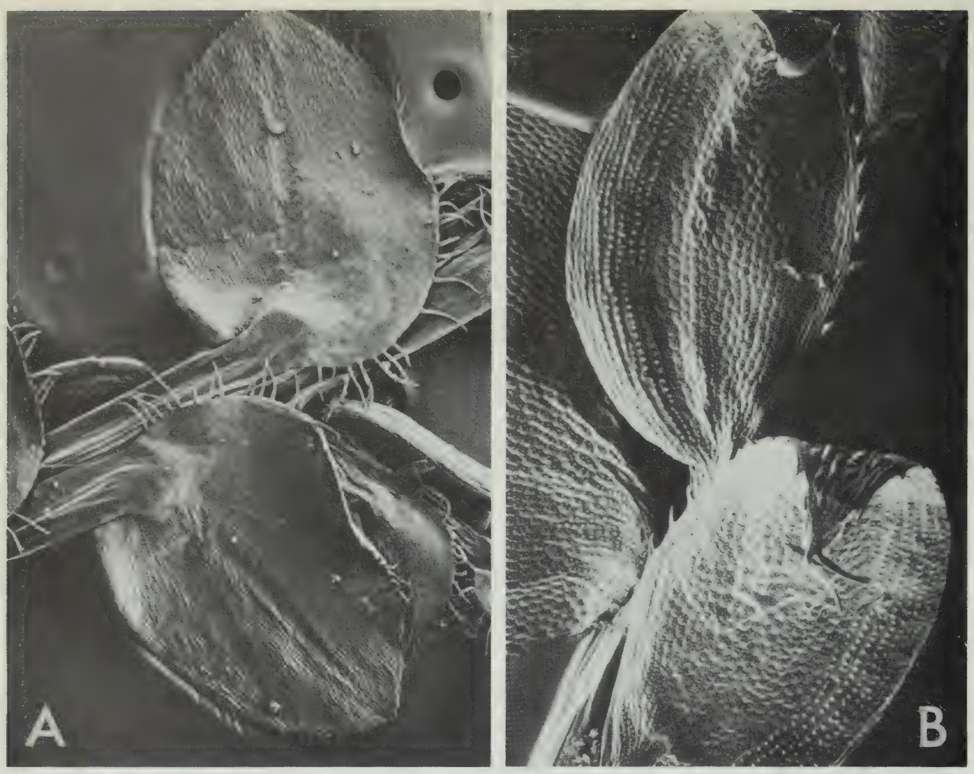

Fig. 16 *Selaginella ovifolia* subsp. *philipsonii* Jermy & Rankin: **A.** Close-up of lateral leaves, × 24. **B.** Close-up of median leaves, × 88. All from *Philipson, Idrobo & Fernandez* 1607a.

Notes: Hieronymous relates *S. cabrerensis* to *S. microphylla*, and *S. daguensis* to *S. apus*, and does not compare them with one another. We can see no difference except that *S. daguensis* is more erect.

85. Selaginella tuberculata Spruce ex Baker in *J. Bot. Lond.* **21** : 83 (1883), *Fern Allies* : 40 (1887); Alston in *Reprium Spec. nov. Regni veg.* **45** : 312 (1936). Type from Brazil: Panuré Falls, Rio Uapes, *Spruce* 2940 (K, holotype; BM, CGE, isotypes).

Specimens seen:
SURINAM. Saramacca : Tafelberg, *Geyskes* 998a (BM); *Maguire* 24339 A (BM).
GUYANA. Essequibo: Kaieteur, *Jenman* s.n. (BM, NY), Waratuk, *Tutin* 480 (BM); between Tukeit and the Kaiteur savanna, *Sandwith* 1278 (BM, K); *Guppy* 168 (BM).
BRAZIL. Amazonas: Type as above.

Geographical range: Sandstone area of Surinam and Guyana to northern Brazil.

Notes: This species differs from *S. rhodostachya* (No. 86), with which Jenman confused it, by its ciliate lateral leaves with tubercles on the lower half of the upper surface.

86. Selaginella rhodostachya Baker in *Timehri* **5** : 221 (1886), in *Trans. Linn. Soc. Lond.* (Bot.) **2** : 296 (1887), *Fern Allies* : 112 (1887). Type from Guyana, Essequibo: foot of Kaieteur Falls, *Jenman* 148 (K, holotype; BM, isotype).
Selaginella brachyclada Baker, *Fern Allies* : 45 (1887). Type from Guyana.
Selaginella diminutifolia Jenman in *Gdnrs' Chron.* III, **2** : 99 (1887). Type from Guyana.
Selaginella brevispicata Hieron. ex Ule in *Bot. Jb.* **52** : 49 (1915), nomen nudum; ex Bautista in *Acta Amazonica* **4** : 19 (1974). Type from Venezuela.

Specimens seen:
GUYANA. Essequibo: type as above; ibid. loc., *Jenman* 1481 (BM, K, type of *S. brachyclada* Baker; NY, type of *S. diminutifolia* Jenman); path to top of Kaieteur Falls, *Jenman* s.n. (NY); Roraima, *Warrington, Burras, Woodhams & Edwards* s.n. (K).
VENEZUELA. Bolívar: Paritepui, 2130 m, *Steyermark* 59836 (BM); Chimanta Massif, Torono-tepui, *Steyermark & Wurdack* 1181 (BM); Mt Roraima, 2255–2620 m. *Steyermark* 58753 (BM, US); *Abbensetts* 1A (BM, K); *Jenman* s.n. (NY); Rondon Camp, 2070 m, *Tate* 466 p.p. (BM, NY); *Ule* 8491 (BM, K; type of *S. brevispicata* Hieron.); *im Thurn* s.n. (BM); summit of Roraima, 270–2740 m, *Steyermark* 58916 (BM).

Geographical range: Confined to southern Guyana and the Roraima massif.

Notes: Specimens which match exactly the type have not been collected since Jenman's original gathering, perhaps because few botanists reach the foot of the Kaieteur. Some other specimens bear rhizophores throughout, and some have slightly narrower leaves. We believe the variation is such that there is a cline to *S. brevispicata* on the upper slopes of Roraima. Baker has dated the British Museum (Natural History) copy of his *Fern Allies* 'July 7' and the *Gardeners' Chronicle* appeared on 23 July 1887.

87. Selaginella potaroensis Jenman in *Gdnrs' Chron.* III, **2** : 154 (1887), *Ferns Brit. W. Indies* : 396 (1909). Type from Guyana, Essequibo: Kaieteur Falls, *Jenman* 1818 (NY, holotype; BM, K, isotypes).

Specimens seen:
GUYANA. Essequibo: type as above; Mt Roraima, Waruma Trail, 1380 m, *Persaud* 124 (UG); between Tukeit and Kaieteur Falls, *Guppy* 164 (BM); *Maguire & Fanshawe* 23083 (BM); *Sandwith* 1275 (BM, K).
SURINAM. Saramacca : Arrowhead Basin; Tafelberg, *Maguire* 24497 (BM, NY).
VENEZUELA. Amazonas: Cerro Duida, 1096–1520 m, *Steyermark* 57999 (BM). Aragua: El Cumbre, Parque Nacional, 1100 m, *Alston* 5318 (BM); La Regresiva, km 25, Parque Nacional, 1000 m, *Williams & Alston* 170a (BM). Lara: Barquisemento, *Moritz* s.n. (BM).

Geographical range: Surinam to Venezuela.

88. Selaginella muscosa Spring in Martius, *Fl. Bras.* **1** (2) : 120 (1840). Type from Brazil: Sebastianopolis, *Luschnatt* s.n. (B ?; not seen).
Lycopodium brasiliense Raddi, *Pl. Bras. Nov. Gen.* : 82 (1825). Type from Brazil.
Lycopodium crassinervium Desv. in *Mém. Soc. linn. Paris* **6** : 190 (1827). Type from Brazil.
Lycopodium pallidum Beyr. ex Gaudich. in Freyc., *Voyage Autour Monde, Bot.*: 285 (1828), nomen abortivum.
Lycopodium albidulum var. *majus* Hook. & Grev. in *Bot. Misc.* **2** : 399 (1831), p.p. Types from Brazil.
Selaginella crassinervia (Desv.) Spring in Martius, *Fl. Bras.* **1** (2) : 119 (1840). Type as above.
Selaginella apus var. *tetragonostachya* Spring in Martius, *Fl. Bras.* **1** (2) : 119 (1840). Type from Brazil.
Selaginella polysperma Spring in *Bull. Acad. r. Belg.* **10** : 138 (1843). Type from Brazil.
Selaginella beyrichii A. Braun, *Index Sem. Hort. bot., Berl.* Appendix **1857**: 16 (1857). Type from cultivated material.
Selaginella anocardia A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 290 (1865). Type from Brazil.
Selaginella brasiliensis (Raddi) A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 290 (1865), non (Desv.) Spring (1838).
Selaginella deltoides A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 287 (1865); Alston in *Reprium Spec. nov. Regni veg.* **45** : 312 (1936). Syntypes from Brazil.
Selaginella brevipes Fée, *Crypt. Brés* : 226 (1869), non A. Braun (1867). Type from Brazil.
Selaginella trifurcata Baker in *J. Bot., Lond.* **21** : 98 (1883), *Fern Allies* : 43 (1887); Alston in *J. Bot., Lond.* **72** : 38 (1934); Knox in *Trans. bot. Soc. Edinb.* **35** : 278 (1950). Type from Brazil.

Selaginella niederleinii Hieron. in *Bot. Jb.* **22** : 418 (1896). Type from Argentina.
Selaginella feei Hieron. in Engl. & Prantl, *Nat. Pflanzenf.* **1** (4) : 713 (1901). Type from Brazil.
Selaginella brasiliensis var. *crassinervia* Hieron. ex Bonap., *Notes Ptérid.* **2** : 137 (1915), nom. nud. Syntypes from Brazil.
Selaginella humilis sensu Hieron. in *Hedwigia* **58** : 321 (1917), non Jenman (1897).

Specimens seen:
GUYANA. Berbice: Sierra Acari, Manicole bog, *Guppy* 336a (BM). Essequibo : Kaieteur gorge, below the falls, *Sandwith* 1478 (BM, K); *Tutin* 535 (BM); Kaieteur savannah, 300 m, *Tutin* 502 (BM).
VENEZUELA. Delta Amacuru : Imataca Mts, *Thompson* 21 (BM).
COLOMBIA. Caqueta : Solano, 8 km SE of Tres Esquinas, on Rio Caqueta below mouth of Rio Orteguaza, 200 m, *Little* 9583 (COL). Magdalena: Mts above Hacienda Cincin, Santa Marta, 2100 m, *Foster & Smith* 1392 (COL). Nariño: between Páramo and Barbacoas, 500 m, *Alston* 8468 (BM). Vaupés: Cerro de Mitú, 250 m, *Schultes & Cabrera* 13931 (COL, US); Raudal Guacurabá between Mitú and Javaraeté, *Schultes & Cabrera* 19268 (US); Rio Vaupes, cachivera de Yurupari, 400 m, *Garcia-Barriga* 14948 (COL).
PERU. Without exact locality: *Hobb* s.n. (BM).
BRAZIL. Without exact locality: *Burchell* 3168 (P); *Glaziou* 1646 (C); 2241 (C, type of *S. brevipes* Fée and *S. feei*, Hieron.), 3543 (C), 4492 (C, P), 4495 (C, P), 4496 (C), 4498 (C, P), 7038 (C), 7354 (C), 9313 (C), 13369 (P); *Richardson* s.n. (BM). Amazonas: near Panure, Rio Uaupés, *Spruce* 2532 (B, type of *S. deltoides* A.Br.; BM, CGE; K, type of *S. trifurcata* Baker); Tutica, Uaupés, *Luetzelburg* 23710 (M). Espirito Santo: *Rambo* 42647 T (BM); Cachoeiro do Itapemim, vargem Alta-Guiomar, *Brade* 19346 (BM); Santa Barbara do Caparao, *Chase* 10075 1/2 (BM). Minas Gerais: Ouro Fino, *Hoehne* 19459 (S); Serra de Antonio Perura, near Ouro Preto, *Silveira* 171 (P); Christina, *Luederwaldt* 20999 (BM). Parana: Serra do Mar, Cadeodo, *Dusen* 654a (C); *Wielewski* 72a (NY), 72 (NY). Santa Catarina: Lagos, *Spannagel* 85A (NY), 85 (BM, NY); Joinville, *Müller* 134 (BM). Rio Grande do Sul: *Jürgens* L 10 (BM); Biopitrade, Santa Cruz, *Stier* L 25 (NY); *Dutra* 227 (BM); Apiahy, *Glaziou* 160 (P); Vila Manresa, *Rambo* 42719 (BM); Rio Pardo, *Jürgens* L 5 (BM); Taquara, *Dutra* 668 (BM); Pareci near Montenegro, *Rambo* 49235 (BM); ad montem Ferrabraz near Hamburg, *Rambo* 43205 (BM); São Leopolodo, *Dutra* 75 (BM), 1607 (BM), 1613 (BM); near Belem Novo, 20 km S of Porto Alegre, *Beetle* 1592 (BM). Rio de Janeiro. *Rudio* s.n. (B, BM); *Glaziou* 13365 (B, C); *Raddi* s.n. (BM); *Gardner* 67 (BM, K. P), 66 (BM, P); *Mosen* 55 (P), 2022 (P); *Brade* s.n. (BM); Tijuca, *Lutz* 1053 (BM); Yucca, Corcovado, *Rose & Russell* 20199 (NY), 20186 (NY); *Murrill* s.n. (NY); Tijuca-Bico, *Alston & Lutz* 307 (BM); Organ mts, *Rose & Russell* 20750 (NY); St Antonio de Finbé, 600 m, *Brade* 11663 (BM); Itatiaia, *Hoehne* 20996 (BM); *Luederwaldt* s.n. (S); *Brade* 10270 (BM), 10051 (BM); 1000 m, *Brade* 17189 (BM); 800 m, *Brade* 18850 (BM); Monte Serrat, near Itatiaia, *Rose & Russell* 20441 (NY); *Hoehne* 24874 (S); Serra do Itatiaia, 800 m, *Brade* 6507 (BM); Itatiaia, estrada Maromba, *Bandeira* s.n. (BM); Teresopolis, cachoeira Teroz, 900–1000 m, *Lutz* 2081 (BM); Theresopolis, Fazenda Cumary a Cachoeira Feroz, 810–840 m, *Lutz* 2107 (BM). Santa Catarina: *MacRae* s.n. (BM): *Schreiner* s.n. (BM). São Paulo: Jundiahy, *Puiggari* 11 (S); José Menino, Santos, *Gehrt* 33427 (BM); Bocaina, *Loefgren* s.n. (SP); Morro do Bahu, *Loefgren & Edwall* s.n. (SP); Nabraya, *Dusén* 2148 (P); Santos, *Mosen* 3125 (C); Jaragua, *Brade* 5137 (NY); Morro de Pedras, *Brade* 7690 (BM, NY); Serra da Cantareira, *Tamandare & Brade* 6598 (NY); Puizzari, *Schwacke* 2384 (BM); Cantareira, *Hoehne* 21027 (BM); Morro das Pedras, Iguape, *Brade* 15719 (BM); Campos do Jordão, *Leite* 3899 (BM); Campo Grande, Serra do Mar, 800 m, *Brade* 6599 (BM).

Geographical range: Tobago, Trinidad and Guyana, west to Colombia and south to northern Brazil; also Argentina, Uruguay and Paraguay.

Notes: S. muscosa is a variable and possibly mixed species that would merit further investigation. Specimens from the Guyanas have been segregated as *S. deltoides* A. Braun; they have lateral leaves which are more triangular, but are otherwise similar. Alston has these segregated as a distinct species but in our opinion the difference is within the range of *S. muscosa*. *Selaginella deltoides* A. Braun was based on *Spruce* 2532 and 2535; isotype material exists in BM and K, but all the material at Berlin belongs to the species subsequently described by Baker as *S. trifurcata* which we believe to be synonymous with *S. muscosa*. *Spruce* 2535 of other herbaria is *S. dendricola* Jenman, i.e. *S. deltoides* sensu Baker. A specimen of *Spruce* 2328, which is *S. cordifolia* (Desv.) Spring, was subsequently

added to the Berlin sheet by A. Braun. *S. crassinervia* and *S. polysperma* were reduced to *S. brasiliensis* by A. Braun (*Annls Sci. nat.* (Bot.) V, **3** : 290; 1865), and *S. beyrichii* (in *Index Sem. Hort. bot., Berl.* Appendix **1857** : 16; 1857). Hieronymus confused this species with *S. humilis* Jenman, which is *S. cladorrhizans* (No. 43). *S. muscosa* may also be confused with *S. cordifolia* (Desv.) Spring but that species has long ciliate lateral leaves and distinctly auricled median leaves. *S. potaroensis* (No. 87) is another similar species, but is distinguished by small unequal-sided median leaves and broad, short platystachyous strobili. *S. flagellata* (No. 41) normally differs by its flagelliform apices and long, narrow, platystachyous strobili.

Lycopodium brasiliense Raddi was the first epithet to be given to this species, but two years later Desvaux (*Mém Soc. linn. Paris* **6** : 190; 1827) described another species by the same name (see *S. flexuosa*, No. 67); that species was combined in *Selaginella* in 1838 thus making the transfer of Raddi's epithet by A. Braun in 1865 illegitimate.

89. Selaginella dendricola Jenman in *Gdnrs' Chron.* III, **2** : 99 (1887); Baker, *Fern Allies*: 70 (1887); Jenman, *Ferns Brit. W. Indies* : 392 (1909); Alston in *Reprium Spec. nov. Regni veg.* **45** : 315 (1936); Knox in *Trans. bot. Soc. Edinb.* **35** : 264 (1950). Type from Guyana, Essequibo: Macouria River, *Jenman* 2323 (NY, holotype; BM, K, isotypes).
Selaginella deltoides sensu Baker, *Fern Allies* : 72 (1887), non A. Braun (1865).

Specimens seen:
FRENCH GUIANA. Guya: Devil's Mts, La Comté R., Boulanger Creek, on rocks near the waterfall, *Leprieur* 243 (BM, P).
SURINAM. Marowijne : Nassau Mts, *Lanjouw & Lindemann* 2628 (BM).
GUYANA. Essequibo: Type as above; Mt Roraima, *Warrington, Burras, Woodhams & Edwards* s.n. (BM, K); Moraballi Creek, *Richards* 19 (K).
COLOMBIA. Vaupés: Cachivera Muriti, Rio Kanararií, 250 m, *Schultes & Cabrera* 14410b (US); Circasia, 240 m, *Schultes & Cabrera* 19684 (US).
BRAZIL. Amazonas: Panure, Rio Uapès, *Spruce* 2535 (BM, CGE, K, US); Cachoeira Cunatí, R. Xie, Rio Negro, *Schultes & Lopez* 9219 (BM).

Geographical range: Colombia to northern Brazil.

Notes: The elongate stem with small distant leaves, alternating with stems with larger closer leaves, is quite distinctive but not shown by all specimens. From *S. producta* (No. 100) this species may be distinguished by its more slender, flexuose, stem, with short filiform rhizophores, thinner texture, stouter strobili, and narrower, proportionately longer, median leaves. *S. seemannii* (No. 63) has a similar texture to *S. dendricola* but the stem is stout, not flexuose, and more regularly pinnate, the lateral leaves are conspicuously costate, and the median leaves are oblique at the base and shortly auriculate on the outer side. Baker applied *S. deltoides* A. Braun to *Spruce* 2535 as represented at Kew and most other herbaria, but Braun's material (in B) is not this plant (see No. 88).

90. Selaginella tenuissima Fée in *Crypt. Vasc. Brés.* **2** : 98 (1873). Type from Brazil: Rio de Janeiro, *Glaziou* 4499 (C).
Selaginella cunninghami Baker in *J. Bot., Lond.* **22** : 110 (1884). Syntypes from Brazil.
Selaginella papagaiensis Silveira in *Bolm Comm. geogr. geol. Minas Geraes* **5** : 125 (1898). Type from Brazil.
Selaginella serpens sensu Fée, *op cit.* : 99 (1873), non (Desv.) Spring (1843).

Specimens seen:
BRAZIL. Without exact locality: *Glaziou* 5217 (BM, syntype of *S. cunninghami* Baker). Minas Gerais: Papagaio, *Silveira* 154 (BM, type of *S. papagaiensis* A. Silveira); Ouro Preto, *Hoehne* 20993 (S); Passa Quatro Itaguaré, 2000 m, *Brade & Araujo* 19040 (BM); Serra do Caparaó, Rio Domingos, 1900 m, *Brade* 17108 (BM). Rio Grande do Sul: Porto Alegre, *Lindman* A517 (BM). Rio Janeiro: type, as above; *Glaziou* 4486 (BM, C, K, L), 4485 (C, K); *Cunningham* s.n. (K, syntype of *S. cunninghami* Baker); Itatiaia, *Hemmendorff* 575 (BM); Terezopolis, *Brade* 9662 (BM); St Antonio de Finbé, *Brade &*

Luis 11666 (BM). Santa Catarina: in einem Erdloche des Laranjiera-Gebirges, *Ule* 131 (BM). São Paulo: Itatiaia, *Hoehne* 20996 p.p. (BM), *Brade* 6508 (NY); Campos do Jordao, 1600 m, *Leite* 3673 (BM).

Geographical range: Endemic to Brazil.

Notes: This is, perhaps, only a slender state of *S. muscosa* Spring.

91. Selaginella falcata (Beauv.) Spring in *Bull. Acad. r. Belg.* **10** : 225 (1843), p.p. excl. planta borbonica in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 181 (1850); p.p. nomen tantum; Alston in *Dansk bot. Ark.* **7** : 200 (1932). Type from French Guiana, without precise locality, *Chastelein* s.n. (OXF).

Plante muscosa et plumosa guayanensis perelegans major Breyn., *Exot. Plant.* : 194 (1678); Ray, *Hist. Plant.* **1** : 119 (1686).

Muscus Americanus, denticulatus, major Tourn., *Inst. Rei Herb.* : 556 (1700), based on Breynius.

Lycopodioides dichostomum taxiforme Dillen., *Hist. Musc.* : 471, t.66 (1742), copied from Breynius.

Stachygynandrum falcatum Beauv., *Prod. Aethog.* : 106 (1805), based on Dillen., t.66, p.p. excl. pl. maurit. et borbon.

Lycopodium falcatum (Beauv.) Desv. in Poiret, *Encycl. Méth. Suppl.* **3** : 540 (1813–4), p.p. excl. pl. maurit. et borbon., in *Mém. Soc. linn. Paris* **6** : 188 (1827), p.p. quoad syn. Schkuhr.

Lycopodium plumosum sensu Schkuhr, *Krypt. Gewächse* **1** : 167 (1809), non L. (1753).

Selaginella breynii Spring in Martius, *Fl. Bras.* **I** (2) : 121 (184), p.p. quoad syn. Breynii; sensu Schomburgk *Reise Brit. Guian.* **3** : 880 (1848), non Spring (1840).

Selaginella guianensis Spring in *Bull. Acad. r. Belg.* **10** : 143 (1843). Type from French Guiana.

Selaginella guayanensis Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 134 (1850); Baker, *Fern Allies* : 56 (1887). Type as above.

Specimens seen:
FRENCH GUIANA. Without precise locality: type, as above; *Leprieur* s.n. (P, type of *S. guianensis* Spring); R. Oyapok, *Leprieur* 161 (BM), 162 (BM). Guya: banks of R La Comte, *Leprieur* 180 (K).

Geographical range: Guyana ? and French Guiana.

Notes: This species has been much confused. The plant figured by Breynius came from French Guiana and there is a scrap at Oxford, collected by Chastelein, which is presumably the type collection. Dillenius seems to have copied the figure of Breynius, and Schkuhr's plate is from a specimen in Herb. Breynius (BM).

Palisot de Beauvois (l.c.: 106) based his species upon the plate of Dillenius, without description, but cited the 'Ile-de-France [Mauritius] et de Bourbon [Réunion]' as localities on p. 113. The plant from Mauritius was *S. concinna* Sw. Though Spring took his name from Breynius, the description was taken from the plant of Martius, now at München. Schomburgk (1848) records it along the Essequibo and Barima in Guyana.

92. Selaginella densifolia Spruce ex Hook. *Second Cent. Ferns* : t.85 (1861); Baker in *J. Bot., Lond.* **21** : 242 (1883), *Fern Allies* : 55 (1887). Type from Colombia, Vichada: Cerro de Mono, between San Fernando and Maypures, *Spruce* 3089 (K, holotype; BM, CGE, LG, isotypes).

Selaginella orinocensis Maury in *J. Bot., Paris* **3** : 130 (1889). Type from Colombia.

Specimens seen:
COLOMBIA. Vicharda: type as above; loc. idem., *Gaillard* 201 (P; type of *S. orinocensis* Maury).

Geographical range: Confined to the Cerrode Mono, Colombia.

Notes: Both Hooker and Baker cited *Spruce* 3809 in mistake for 3089, and Cerro de Morro for Cerro de Mono. The type of *S. orinocensis* seems to have been collected in precisely the same spot as Spruce's type, but the stems are broader and the leaves slightly acuminate, showing some characterstics of *S. kochii* (No. 93). Typical *S. densifolia* has the lateral leaves tightly curled around the stem, especially on the primary branches, when dry, and in the young shoot they are dense and tend to curl upwards in a characteristic manner.

The Spruce reference (*Notes of a Botanist in the Amazonian Andes* **1** : 454; 1908) to a 'Selaginella bearing some resemblance to a closely cut box-edging' was most likely to this species.

93. Selaginella kochii Hieron. in Koch-Grünberg, *Reisen in Nordwest-Brasilien* **2** : 361 (1910), in *Reprium Spec. nov. Regni veg.* **8** : 151 (1910); Knox in *Trans. bot. Soc. Edinb.* **35** : 281 (1950). Type from Brazil, Amazonas: Cachoeira Borédao, Rio Negro, *Koch* 21 p.p. (B, holotype; BM, isotype).

Selaginella densifolia sensu Alston in Pulle, *Fl. Surin.* **1** : 170 (1938), non Spruce.

Specimens seen:
SURINAM. Nickeri: Upper Sipaliwini, camp IX, *Rombouts* 326 (BM).
VENEZUELA. Amazonas: Piedra de Cocui, Rio Negro, *Schultes & Lopez* 9430 (BM).
COLOMBIA. Caqueta: Florencia, *Perez Arbelaez* 642 (BM, US); Solano, 8 km SE of Tres Esquinas, on Rio Caqueta below mouth of Rio Orteguaza, 200 m, *Little* 9713 (COL), 9545 (COL). Meta: near Villavicencio, 500 m, *Perez Arbelaez* 182 (BM); *Alston* 7538 (BM). Valle del Cauca: El Silencio, Yanaconas, 1900—2200 m, *Killip & Garcia* 33746 (COL). Vaupés : Rio Kuduyari, Cerro Yapoboda, 450 m, *Schultes & Cabrera* 14172 (COL); Cerro Yapobodà, 45 m, *Schultes & Cabrera* 14174 (US); Cerro Isibukuri, 250–700 m, *Schultes & Cabrera* 13316 (US, COL).
BRAZIL. Amazonas: type, as above; Serra de São Gabriel, Rio Negro, *Schultes & Lopez* 9176 (BM); Serra Curicuriari, *Schultes & Lopez* 9827 (BM); Serra Wabeesee, Rio Uaupés, *Schultes & Pires* 9134 (BM).

Geographical range: Amazon basin from Surinam to Colombia.

Notes: The Rombouts specimen from the Upper Sipaliwini is smaller but more like this species than *S. densifolia* (No. 92).

94. Selaginella truncata Karsten ex A. Braun, *Index Sem. Hort. bot., Berl.* Appendix **1857** : 15 (1857), in *Annls Sci. nat.* (Bot.) IV, **13** : 65 (1860), *op. cit.* V, **3** : 273 (1865); Baker, *Fern Allies* : 53 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 281 (1950). Syntypes from Colombia, Cundinamarca: Bogota, Andes of New Grenada, *Karsten* s.n. (B, BM); Susumuco, 1000 m, *Triana* 696 (BM); 238 (NY).

Selaginella weberbaueri Hieron. ex Knox in *Trans. bot. Soc. Edinb.* **35** : 282 (1950).

Specimens seen:
VENEZUELA. Without exact locality: Burro, S. Esteban, *Goebel* 1889 (P).
COLOMBIA. Boyaca: Labranzegrande, 1150 m, *Guevara Amortegui* 345 (BM, US). Cundinamarca: syntypes as above; Bogota, *Triana* s.n. (US). Meta: near Villavicencio, 5–600 m, *Perez Arbelaez* 182 [bis] (BM, US); *Haught* 2524 (BM); *André* 807 (NY); *Alston* 7612 (BM); Los Llanos, Villavicencio, hacia El Parrao, 500 m, *Cuatrecasas* 4601 (COL); Los Llanos del Rio Guatiquia, near Villavicencio, 350 m, *Molina & Barkley* 18M.055 (COL, UC); Llanos Orientales, Santa Isabel, between Restrepo and Cumaral, 450 m, *Garcia-Barriga* 5010 (AAU).
PERU. Loreto: Mt Guayrapurima, Tarapot, *Spruce* 4024 (BM, CGE, NY).
BOLIVIA. La Paz: San Antonio near Mapiri 850 m, *Buchtien* 1070 (BM, US); *Buchtien* s.n. (Rosenstock exsicc. 95; BM); San Carlos 750 m, *Buchtien* 54 (US).

Geographical range: Colombia and Venezuela to Peru and Bolivia.

Notes: Incomplete specimens may be confused with *S. cruciformis* (No. 53), which has thicker, less flexuose, stems, more oblong median leaves, and lateral instead of terminal

strobili. *S. breynii* (No. 97) has a similar habit, but the median leaves are aristate. *S. applanata* (No. 98) is a smaller plant with the median leaves always ciliate and aristate.

95. Selaginella homaliae A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 274 (1865); Baker, *Fern Allies* : 53 (1887); Alston in *Reprium Spec. nov. Regni veg.* **45** : 315 (1936). Syntypes from Brazil, Amazonas: Cataracts of Jaruma and Panure, Upper Amazon, *Spruce* 2534 (BM, CGE, K); *Spruce* 2941 (K); Cachoeira da Tarumu, *Traill* 1437 (K).

Specimens seen:
COLOMBIA. Vaupés: Rio Vaupés, Circasia, 240 m, *Schultes & Cabrera* 19695 (US, COL).
BRAZIL. Amazonas: syntypes as above.

Geographical range: Colombia and northern Brazil.

Notes: This species closely resembles *S. applanata* (No. 98) in habit, but the median leaves are aristate on that species, and their apices are directed forwards instead of overlapping the stem.

96. Selaginella calosticha Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 206 (1850); Baker, *Fern Allies* : 55 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 280 (1950). Type from Venezuela, Federal District: Caracas, 1500 m, *Funck & Schlim* 3321 (K).

Specimens seen:
VENEZUELA. Federal District: Type as above; Caracas, *Funck & Schlim* 3320 (BM); Galipan, 1200 m, *Funck & Schlim* 335 (BM, C); 3352 (W).
PERU. San Martin: Tingo Maria, 625–1100 m, *Allard* 20821 (BM), 21206 (BM).

Geographical range: Venezuela and Peru.

Notes: The microspores have capitate papillae, but the larger size and closer leaves appear to distinguish this species from *S. tarapotensis* (No. 99), which is otherwise very similar.

97. Selaginella breynii Spring in Martius, *Fl. Bras.* **1** (2) : 121 (1840), p.p. excl. syn. Breyn.; in *Mém. Acad. r. Sci. lett. Belg.* **24** : 119 (1850), p.p. quoad *Schomburgk* 982 et spec. *Martius*; Baker, *Fern Allies* : 54 (1887), p.p. excl. syns Schkuhr et Dillen.; Knox in *Trans. bot. Soc. Edinb.* **35** : 279 (1950). Type from Brazil, *Martius* s.n. (M).
Selaginella panamensis Linden, *Cat.* **10** : 22 (1855), nom. nud.
Lycopodium concinnum sensu J. Smith in *J. Bot., Lond.* **1** : 203 (1842), non Sw.
Selaginella concinna sensu Schomb., *Reise in Guiana* **3** : 880, 1042 (1848), non. (Sw.) Spring (1838) nec Baker (1891).

Specimens seen:
COLOMBIA. Santander: near Barracan Bermeja, 100–500 m, *Haught* 1339 (BM); km 6 between Puerto Wilches and Puerto Santos, 100–115 m, *Killip & Smith* 14872 (NY). Meta: Pico Renjifo, Serra de la Macarena, *Philipson, Idrobo & Jaramillo* 2162 (BM); *Idrobo & Schultes* 1151 (BM).
BRAZIL. Without precise locality: type as above; *Glaziou* 14414 (BM); Serra de Jurutz, *Traill* 1432 (K). Amapa: Oiapoque, *Black* 8275 (BM); Igarapé Pontanarré Rio Oiapoque, *Froes* 26005 (BM). Amazonas: near Manaos, *Spruce* s.n. (BM, C); Cararaucu, *Traill* 1434 (K); Conoceicao, Rio Negro, *Traill* 1433 (K); forest on Rio Marnelhos, R. Madeira, Barra, Rio Negro, *Spruce* s.n. (BM, CGE); Cachveira Tamura, Manaos, *Occhioni* 69 (BM); Igarape do Gnedes, *Kuhlmann* 998 (BM); Rio Apahu, *Hübner* 56 (BM). Bahia: Säo Bento, *Luetzelburg* 304 (BM). Para: Rio Padauiri, *Schomburgk* 982 (BM); Rio Aripecuru, *Spruce* s.n. (BM, CGE); Santarem, *Spruce* s.n. (CGE).

Geographical range: Brazil and Colombia.

Notes: The plant from Rio Aripecuru is smaller, as are the specimens from Colombia. The record for British Guiana (sub. *S. concinna*) appears to be based on the Schomburgks Brazilian specimen. Spring's record for the Orinoco was based on the same specimen, and his Chilean record refers to a specimen of a Philippine species wrongly localised in Haenke's collection.

98. Selaginella applanata A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 274 (1865). Type from Peru, Puño: near San Gaven, *Lechler* 2405 (K; BM, fragment).
Selaginella jungermannioides sensu Baker, *Fern Allies* : 53 (1887), p.p. quoad pl. peruviana, non (Gaudich.) Spring (1843) nec Zoller (1854).

Specimens seen:
COLOMBIA. Caquetá: Morelia, 300 m, *v. Sneidern* A1291 (S).
PERU. Puño: type as above.

Geographical range: Colombia and Peru.

99. Selaginella tarapotensis Baker in *J. Bot., Lond.* **21** : 98 (1883), *Fern Allies* : 44 (1887). Type from Peru, Loreto: Mt Guayrapurima, near Tarapoto, *Spruce* 4625 (K, holotype; BM, CGE, US, isotypes).

Specimens seen:
COLOMBIA. Caldas: La Selva, Pueblo Rico, 1500 m, *v. Sneidern* 5517 (S). Meta: Cordillera Macarena, 1300–1900 m, *Schultes* 12120 (BM), 12123 (BM, UC), 12125 (BM, UC); *Idrobo & Schultes* 1054 (BM, COL), 1055 (BM, COL), 1077 (BM, COL), 1091 (BM). Nariño: below Paramo, 1000 m, *Alston* 8552 (BM).
ECUADOR. Santiago-Zamora: Rio Itzintza, Cordillera Cutucu, 1050–1110 m, *Camp* E 1221 (BM).
PERU. Loreto: type as above. San Martin: near Tingo Maria, 846M, *Allard* 21390 (BM). Junin: Schunke Hacienda, above San Ramon, 1300–1700 m, *Schunke* A 246 (BM, US); Chanchamayo Valley, *Schunke* 195 (BM). Cuzco: Sapansachayoc, Paucartambo, 950 m, *Vargas* 7350 (BM).
BOLIVIA. La Paz: Santa Barbara, 1650 m, *Williams* 1401 (NY, US); Ticunhuaya, 1500 m, *Tate* 1077 (US); Hacienda Simaco, on way to Tipuani, Larecaja, 1400 m, *Buchtien* 5276, (BM, NY, US), 5283 (BM, NY, US); Polo-Polo, near Coroico, N Yungas, *Buchtien* s.n. (US); San Antonio, Chapiri, 850 m, *Buchtien* 1045 (US), 1071 (BM, US); San Carlos, Mapiri, 850 m, *Buchtien* 55 (US), 56 (NY, US), 58 (NY), 59 (NY), 1078 (BM, US); above Mapiri, 1200 m, *Williams* 1406 (NY, US); Mapiri, 750 m, *Rusby* 461 A (NY).

Geographical range: Mexico to Bolivia.

100. Selaginella producta Baker in *J. Bot., Lond.* **21** : 243 (1883), p.p., *Fern Allies* : 56 (1887), p.p. excl. pl. Lindbergi; Knox in *Trans. bot. Soc. Edinb.* **35** : 262 (1950). Types from Guyana: *Appun* 196, 198; *Drake* s.n. (K); and Brazil, Amazonas: between Barcellos and San Gabriel, *Spruce* 2043 (BM, holotype; CGE, isotype); Minas Gerais, *Lindberg* s.n. (K).
Selaginella cayennensis Baker, *Fern Allies* : 44 (1887). Type from French Guiana.
Selaginella tobagensis Hieron. in *Symb. Antill.* **3** : 524 (1903). Type from Tobago.
Selaginella tarumensis Hieron. ex Bonap., *Notes Ptérid.* **1** : 180 (1915), nom. nud.

Specimens seen:
SURINAM. Saramacca: Nassau, *Lanjouw & Lindeman* 2579 (BM), 2792 (BM); between Pakka-pakka and Ebbatop, *Florschutz* 1350 (BM); Tafelberg, *Maguire* 24316 (BM).
FRENCH GUIANA. Guyane: Bradel Falls, R. le Comté, *Leprieur* 157 (BM, K, P; type of *S. cayennensis* Baker); covering the rocks at the Bradel, *Leprieur* 242 (P); Cacao Creek, R. le Comté, *Leprieur* 156 (P).
GUYANA. Without exact locality: syntypes as above; between Demerara and Berbice Rivers, *De la Cruz* 1609 (NY); region of Mt Raywa, *Jenman* s.n. (NY); near Mt Arisaru, *Guppy* 29 (BM), 38 (BM). Berbice: Sierra Acarai Region, Bay forest, 5 miles East of Onoro, *Guppy* 243 (BM); Sierra Acarai Region, Upper Chodiker, *Guppy* 461 (BM). Demerara: Great Falls, Demerara R, *Jenman* s.n. (NY); *Beccari* s.n. (FI); Demara R, *Jenman* s.n. (NY), 4212 (BM); Werebaru Creek to Baboon camp, *Beccari* s.n. (FI); Baboon camp, Demerara R, *Beccari* s.n. (FI); Canister Falls, Waini R, *Beckett* s.n. (BM). Essequibo: Sebai Creek, Kaituma R, *Fanshawe* 2417 (BM); Kanuku Mts, Takubu R, *A. Smith* 3293 (BM); Macouria creek, Essequibo R, *Jenman* s.n. (NY); 2325 (BM); Bartica to Potaro Rd, near 14 m to post, *Sandwith* 1139 (BM, K); Moraballi Creek, near Bartica, *Richards* 268 (BM, K) 196 (BM, K); near Dadanawa, Upper Rupununi, *De la Cruz* 1810 (NY); Junction of Mazuruni and Cuyuni rivers *Graham* 315 (NY); Mazuruni R, near First Falls, *Sandwith* 1168 (BM, K); Upper Mazuruni R, *De La Cruz*

2188 (NY, K); Eagle Mt, Potaro R. *Jenman* s.n. (BM, NY); Tumatumari, Potaro R, *Gleason* 63 (NY); Tiger Creek, Tumatumari, *Tutin* 548 (BM); Potaro R, *Jenman* s.n. (NY); Kaieteur Gorge, *Tutin* 523 (BM); *Sandwith* 1477 (BM, K); between Tukeit and Kaieteur Plateau, *Maguire & Fanshawe* 23089 (BM), *Guppy* 162 (BM).

VENEZUELA. Delta Amacuro: Lower Orinoco, *Rusby & Squires* 438 (BM, NY), 439 (BM, NY); Imataca Mts, *Thompson* 18 (BM).

COLOMBIA. Amazonas: Randal Yayacopi, Rio Apaporis, 240 m, *Schultes & Cabrera* 16216 (US); Cerra de la Cente Chiquita, *Schultes & Cabrera* 16497 (BM, US). Nariño: Buenaventura, *André* 252 (NY). Santander: near Barranca Bermeja, 100–500 m, *Haught* 1338 (BM).

PERU. Loreto: Iquitos, 100 m, *Killip & Smith* 27322 (BM, NY); Mishuyacu, 100 m, *Klug* 198 (BM, NY, US).

BRAZIL. Without exact locality: *Glaziou* 10212 (C), 10215 (C). Amazonas: syntype as above; without further locality, *Schwacke* s.n. (BM); Taruma rapids near Barra, *Spruce* 4731 (BM, CGE, US; type of *S. tarumensis* Hieron.); *Occhioni* 20220 (BM). Goias: Corrego Alogado, *c.* 30 km, SW of Brasilia, 1000 m, *Irwin, Grear, Souza & Reis dos Santos* 14056 (BM, NY); Corrego Itaquera, *c.* 30 km N of Formosa, 850 m, *Irwin, Souza, Grear & Reis dos Santos* 15573 (BM, NY). Parana: Palmeira, *Freitas* 55 (BM, NY).

Geographical range: Tobago and Trinidad to French Guiana, west to Colombia and south to Brasilia and northern Peru.

Notes: S. revoluta (No. 102) is superficially similar but easily separated by the long cilia at the base of the lateral leaves. These lateral leaves are often inrolled and are usually smaller, narrower and more acute than the median leaves. *S. seemannii* (No. 63) is similar in habit, but the lateral leaves are thinner with a distinct costa, and the median leaves gradually acuminate rather than abruptly aristate, with oblique auriculate bases. *S. cayennensis* Baker is a small form, and is matched by *Tutin* 548 from wet rocks in Guyana; it is within the range of the species.

101. Selaginella macrostachya (Spring) Spring in *Bull. Acad. r. Belg.* **10** : 144 (1843). Type from Brazil, without exact locality, *Sellow* s.n. (K).

Selaginella flexuosa subsp. *macrostachya* Spring in Martius, *Fl. Bras.* **1** (2) : 123 (1840). Type as above.

Selaginella gardneri Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 134 (1850). Type from Brazil.

Selaginella ericoides Fée, *Crypt. Vasc. Brés.* : 228 (1869); Hieron. in *Hedwigia* **43** : 38 (1903). Type from Brazil.

Selaginella geminata Fée, *Crypt. Vasc., Brés., Suppl.* : 100 (1873). Type from Brazil.

Selaginella lindbergii Baker in *J. Bot., Lond.* **21** : 99 (1883). Type from Brazil.

Selaginella henriqueana Silveira in *Bolm Comm. geogr. geol. Minas Geraes* **5** : 123 (1898). Type from Brazil.

Specimens seen:

BRAZIL. Without exact locality: type as above; *Glaziou* 2243 (BR, type of *S. ericoides* Fée), 4500 (C). Minas Gerais: *Lindberg* s.n. (K, type of *S. lindbergii* Baker); near Chora, *Silveira* 163 (BM). Rio de Janeiro: *Glaziou* 4484 (C, K, type of *S. geminata* Fée); Alto Macahe, *Glaziou* 7281 (BM, C, P), 7282 (BM, P); Serra das Orgãos, *Gardner* 5958 (K, type of *S. gardneri*); Serra dos Orgãos Corrigo Berjaflos, 1300 m, *Brade* 16585 (BM); Teresopolis, *Brade* 9444 (BM); Teresopolis, Cachoeira Teroz, 900–1000 m, *Lutz* 2080 (BM). Santa Catarina: Fachinal Biguassu, *Rambo* 50372 (BM); Brusque, 50 m, *Reitz* 3144 (BM); Morro Queimadas, *Spannagel* 212 (NY); Alto da Serra, *Bauer* 81 (NY). São Paulo: Alto da Serra, *Brade* 5851 (BM); *Hoehne* 4735 (BM), 28172 (S); *Gehrt* s.n. (BM); *Edwall* s.n. (BM); *Luederwaldt* 21034 (S); Parque Cazuru, *Luederwaldt* 1657 (BM); Santos, *Mosen* 3758 (C); Serra do Itatins, Iguape, 800 m, *Brade* 8627 (BM).

Geographical range: Confined to southern Brazil.

102. Selaginella revoluta Baker in *J. Bot., Lond.* **21** : 141 (1883), *Fern Allies* : 46 (1887); Alston in Pulle, *Fl. Surinam* **1** : 169 (1938); Knox in *Trans. bot. Soc. Edinb.* **35** : 260

(1950). Type from Venezuela, Amazonas: near Maupures, *Spruce* 3621 (K, holotype; BM, CGE, US, isotypes).

Selaginella platybasis Baker in *J. Bot., Lond.* **21** : 242 (1883), *Fern Allies* : 54 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 262 (150). Type from Brazil.

Selaginella demissa Christ in *Bull. Herb. Boissier* II, **1** : 75 (1901). Type from Peru.

Specimens seen:

FRENCH GUIANA. Without precise locality, *Leprieur* s.n. (NY, P). Inini: Upper Oyapok, *Leprieur* 4 (NY, P); Naneteri, Upper Oyapok, *Leprieur* 169 (P).

SURINAM. Nickerie: Nickerie R., *Tulleken* 377 (L, U). Saramacca: Wilhelminagebergte, *Stahel* 335 (U), 482 (U).

GUYANA. Essequibo: Eagle Mt, Potaro R, *Jenman* s.n. (BM, NY); Tiger Creek, Tametumari, *Tutin* 544 (BM); Garroway stream Potaro River gorge, *Maguire & Fanshawe* 22971 (BM).

VENEZUELA. Amazonas: type, as above; Rios Pacimoni-Yatua, Casiquiare, on Piedra Aravicava, 110—200 m, *Maguire, Wurdack & Bunting* 37458 (BM); Bolívar: salto de Para, Medico Caura, 300 m, *Williams* 11379 (BM).

COLOMBIA. Caqueta: Florencia, *Perez Arbelaez* 668 (BM, US). Meta: Rio Guapaya, Macarena, 450 m, *Philipson, Idrobo & Fernandez* 1607 (BM, COL). Nariño: Buenaventura, *André* 273 (NY). Valle del Cauca: Cali-Buenaventure Highway, 100 m, *Haught* 5320 (BM, COL). Vaupés: below Teresita, Rio Papurí, *Schultes & Cabrera* 19484 (US); Caño Paca, Río Piraparaná, *Schultes & Cabrera* 17595a (BM, US); Soratama, between Río Pacoa & Río Kananarí, *Schultes & Cabrera* 13022 (US), 13751 (US).

PERU. Loreto: Rio Mayo, near Tarapoto, *Spruce* 4732 (BM); Mishuyacu, near Iquitos, 100 m, *Klug* 1220 (BM, NY, US); Gametanacocha, Rio Mazari, 100–125 m, *Schunke* 322 (BM, UC); Ucayali, *Huber* s.n. (P, type of *S. demissa*). San Martin: near Tingo Maria, 625–1100 m, *Allard* 20415 (BM), 20485 (BM), 22396 (BM).

BRAZIL. Amazonas: San Gabriel de Cachoeira, *Spruce* 2195 (BM, CGE); Panure on Rio Uapes, *Spruce* 2502 (BM, type of *S. platybasis*); summit of Serra Curicuriari, *Schultes & Lopez* 9839 (BM).

Geographical range: French Guiana to Panama south to 10°S latitude.

Notes: This species has the habit of *S. producta* (No. 100) but is separated by its ciliate, tapering, and more acute, lateral leaves. The leaves are sometimes slightly pubescent on the upper surface near the margins (e.g. *Tutin* 544).

103. Selaginella porelloides (Lam.) Spring in *Bull. Acad. r. Belg.* **10** : 141 (1843); Hieron. in *Hedwigia* **43** : 298 (1917). Type from 'Croît dans les Antilles' (P, not seen).

Lycopodium porelloides Lam., *Encycl.* **3** : 652 (1791). Type as above.

Stachygynandrum porelloides (Lam.) Beauv., *Prodr. Aethog.* : 110 (1805). Type as above.

L. anomalum Hook. & Grev. in Hook., *Bot. Misc.* **2** : 400 (1831). Type from Guyana.

S. anomala (Hook. & Grev.) Spring in *Bull. Acad. r. Belg.* **10** : 232 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 247 (1850); Baker, *Fern Allies* : 122 (1887). Type as above.

S. platyphylla Baker in *J. Bot., Lond.* **23** : 294 (1885), *Fern Allies* : 121 (1887), non Veitch (1882). Type from Guyana.

S. platyphylla var. *laxa* Jenman, *Ferns Brit. W. Indies* : 389 (1909). Type from Guyana.

S. jenmani Baker, *Fern Allies* : 45 (1887), in *Gdnrs' Chron.* III, **2** : 154 (1887). Type from Guyana.

Specimens seen:

FRENCH GUIANA. Without precise locality: *Leprieur* s.n. (NY), 168 (BM, P); Oyapock, *Leprieur* s.n. (P); Karouany, *Sagot* 749 (BM, NY, P). Guyane: stream at base of Mt Matouri, Cayenne Isl., *Leprieur* 165 (K); Maroni, Portal Isl., *Sagot* 1123 (K); bank of R Sourou, R la Comté, *Leprieur* 167 (P); near Cayenne, *Mille* s.n. (P).

GUYANA. Without precise locality: *Jenman* 1818 (K), 1819 (K, type of *S. platyphylla* var. *laxa* Jenman); Mt Raywa, *Jenman* s.n. (NY). Demerara: Upper Demerara R, *Jenman* s.n. (BM, K, syntype of *S. platyphylla* Baker; NY); Kara Kara Creek, Demerara R, *Jenman* s.n. (NY); Demerara, *Ankers* s.n. (K, type of *S. anomala* Spring). Essequibo: Bartica Grove, *Jenman* 2322 (BM); Baracaa, Mazaruni, Essequibo R, *Barkly* s.n. (BM); between Demerara and Berbice rivers, *De la Cruz* 1608 (NY); Kaieteur ravine, *im Thurn* 78 (K, syntype of *S. platyphylla* Baker); ravines near Kaieteur Fall, *Jenman* s.n. (NY);

ravines near Kaieteur savannah, *Jenman* 1482 (K); foot of the Kaieteur, *Jenman* 1480 (BM, K, type of *S. jenmani* Baker; NY); between Tukeit and the Kaieteur savannah, *Sandwith* 1452 (BM, K); Upper Rupununi, near Dadanawa, *De la Cruz* 1529 (NY); near Bartica, Essequibo R, *De la Cruz* 1935 (NY); forest opposite Bartica, *Jenman* s.n. (NY); Macouria creek, Essequibo, *Jenman* s.n. (NY); *Sandwith* 1568 (BM, K); H.M.P.S., near Kartabo, Essequibo R, *Guppy* 1 (BM); Mazaruni Station, *Tutin* 62 (BM).

Geographical range: Confined to the Guianas.

104. Selaginella exaltata (Kunze) Spring in *Bull. Acad. r. Belg.* **10** : 234 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 145 (1850); Baker, *Fern Allies* : 93 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 270 (1950). Type from Peru, San Martin: ab Uchiza ad Tocoche, *Poeppig* 1953 (syntypes ?B, LG; not seen).

Lycopodium exaltatum Kunze in *Linnaea* **9** : 8 (1835). Type as above.

Selaginella strobilifera Christ in *Bull. Herb. Boissier* II, **1** : 72 (1901), in *Hedwigia* **45** : 194 (1906). Type from Peru.

Specimens seen:

COLOMBIA. Amazonas: Hervinha, Loreto-Yaco, *Black & Schultes* 46–258 (BM); Caño Guacaya, Rio Miritiparana, 215 m, *Schultes & Cabrera* 16568 (US). Antioquia: Vijagual, S of Turbo, 40 m, *Haught* 4555 (BM). Chocó: Rio Juradó, 100 m, *v. Sneidern* A 184 (S); Rio Truando, *Schott* 5 (NY). Nariño: Barbacoas, *Alston* 8504 (BM); Pambana, Rio Telembi, 50 m, *Ewan* 16833 (BM); Costa del Pacifico, Herrara, Candelillas 30–100 m, in valley of Rio Mira, *Idrobo & Weber* 1392 (COL). Putumayo: Puerto Ospina, *Schultes & Cabrera* 18945 (US).

ECUADOR. Without exact locality: *Fraser* s.n. (BM); Esmeraldas, *Sodiro* s.n. (NY). Napo-Pastaza: Archedona, *Jameson* 708 (BM); 650 m, *Mexia* 7281 (BM); Tena, *Asplund* 8893 (S); Vera Cruz on Rio Indillama, *Asplund* 19448 (S); Puerto Francisco de Orellana 300 m, *Balslev & Madsen* 10604 (BM).

PERU. Junín: between Azupizu and Santa Rosa, 650 m, *Killip & Smith* 26136 (BM, NY); Puerto Bermudez, 375 m, *Killip & Smith* 26498 (BM, NY). Loreto: Santa Rosa, Rio Huallaga, 135 m, *Killip & Smith* 28776 (BM, NY); between Yurimaguas and Balsapuerto, 135–150 m, *Killip & Smith* 28088 (BM, NY); Rio Huallaga, 155–210 m, *Williams* 4825 (BM); Pebas, *Williams* 1600 (BM).

BRAZIL. Without exact locality, *Glaziou* 10216 (C). Acre: Haradouro do Abunam, *Kuhlmann* 1722 (BM). Amazonas: Monte Verde, Rio Purus, *Huber* 4555 (BM).

Geographical range: Panama, south to Peru and western Brazil.

Notes: Spring (1850) states that the stems may be up to 18 m long. *Asplund* (on specimen no. 8893) notes 'scandent to a height of 3 m'; other collectors give lower figures.

105. Selaginella tomentosa Spring in *Mém. Acad. r. Belg.* **24** : 231 (1850). Knox in *Trans. bot. Soc. Edinb.* **35** : 290 (1950). Type from Colombia, Cauca: Gorgona Isl., *Hinds* s.n. (K).

Selaginella geniculata var. *tomentosa* (Spring) Baker in *J. Bot., Lond.* **23** : 121 (1885), *Fern Allies* : 105 (1887). Type as above.

Selaginella ferruminata sensu Seemann, *Bot. Herald* : 243 (1855), non Spring (1843). Type from Peru.

Specimen seen:

COLOMBIA. Antioquia: Rio Ampurrumiado, 200 m, *Gutiérrez & Barkley* 17C151 (BM). Cauca: Isle of Gorgona, *Barclay* 902 (BM); *Cheesman* 26 (BM); type as above. Chocó: Bay of Chocó, *Seemann* 1005 (BM). Vallee del Cauca: bridge over Dagua, near Buenaventura, *Alston* 8634 (BM).

ECUADOR. Santiago-Zamora: Cordillera Cutucú, *Camp* E 1066 (BM). Tungurahua: Volcano Tungurahua, *Sodiro* s.n. (NY).

Geographical range: Confined to Colombia and Ecuador.

106. Selaginella conduplicata Spring in Martius, *Fl. Bras.* **1** (2) : 129 (1840); in *Flora, Jena* **21** : 200 (1838), nom. nud., in *Mém. Acad. r. Sci. Lett. Belg.* **34** : 229 (1850), p.p. quoad pl. bras. Type from Brazil, Para, *Martius* s.n. (M).

Selaginella stellata Spring in Martius *Fl. Bras.* **1** (2) : 129 (1840), p.p. non Spring (1838), *Mém. Acad. r. Sci. Lett. Belg.* **24** : 228 (1850); sensu Alston in *Reprium Spec. nov. Regni veg.* **40** : 309 (1936); sensu Pulle, *Fl. Surinam* **1** : 163 (1938). Type from Brazil.
Selaginella calcarata A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 305 (1865). Type from Brazil.
Selaginella parkeri var. *stellata* (Spring) Baker in *J. Bot., Lond.* **23** : 120 (1885), *Fern Allies* : 104 (1887). Type as above.

Specimens seen:
FRENCH GUIANA. Guyane: Cayenne, *Leprieur* s.n. (NY), *2* (P); *Porteau* s.n. (K). Inini: Rio Gabaret, Oyapok, *Leprieur* 174 (K).
SURINAM. Without precise locality: *Focke* 1217 (K, U). Marowijne: Rio Corentyne near Poelegoedoe, *Versteeg* 633 (U).
COLOMBIA. Amazonas: Cano Guacaya, Rio Miritiparana, 215 m, *Schultes & Cabrera* 16394 (US). Santander: near Barranca Bermeja, Magdalena Valley, between Sogamoso and Colorado Rivers, 100—500 m, *Haught* 1266 (BM). Vaupés: Cerro de Mitú, 250 m, *Schultes & Cabrera* 13937 (US); Cachivera Palito, Rio Kananari, 250 m, *Schultes & Cabrera* 13177 (BM, US); Yapaboda, Rio Kuduyari, 275–305 m, *Schultes & Cabrera* 20028 (US); Rio Kuduyari, 215–245 m, *Schultes & Cabrera* 20020 (US); Lagunas del Churucho, Rio Apaporis, 280 m, *Garcia* 13661 (BM); Cachivera de Jirijirimo, Rio Apaporis, 250 m, *Schultes & Cabrera* 12438 (COL, US); Rio Pacoa, tributary Rio Apaporis, 900 m, *Schultes & Cabrera* 15200 (COL, US); Soratama, Rio Apaporis, 275 m, *Schultes & Cabrera* 15020 (COL, US); Rio Vaupés, Cerro Mitú, *Schultes & Cabrera* 17827 (COL); Rio Apaporis, Soratama, *Schultes & Cabrera* 16150 (COL).
PERU. Loreto: Iquitos, *Asplund* 13939 (S); Mishuyacu, near Iquitos, 100 m, *Klug* 150 (NY); Iquitos, *c.* 100 m, *Killip & Smith* 26937 (BM), 27030 (BM, NY), 27376 (BM, NY); trail to San Juan, Iquitos, *Mexia* 6496 (BM); Amazon River, near Iquitos, 120 m, *Williams* 8237 (BM).
BRAZIL. Without exact locality: *Lippald* s.n. (BM); *Burchell* 9436–2 (K), 9269 (K). Amazonas: *Glaziou* s.n. (BM); Manaos, *Kuhlmann* 980 (BM); *Killip & Smith* 30101 (BM); *Krukoff* 8015 (BM); Beach Taraina, Manaos, *Solomon* s.n. (BM); Cerro Dimiti, Rio Negro, *Schultes & Lopez* 9950 (BM); mouth of Rio Xié, *Schultes & Lopez* 9203 (P); São Manoel, Rio Tapajoz, *Kuhlmann* 67 (BM); Rio Taruma, *Froes* 24860 (BM, IAN); Aurura, Manaos, *Luetzelburg* 22065 (M); Muyrapenima, Rio Negro, *Tate* 56 (NY); Manaos, *Killip & Smith* 30101 (BM); Aranja, R Uruara, *Traill* 1422 (K). Para: Thomé Assu, Rio Assu, 35 m, *Mexia* 6003 (BM); Para, *Home* s.n. (BM); *Smith* 11005 (BM); *Spruce* s.n. (BM, CGE); *Ridley, Lea & Ramage* 36 (BM); *Huber* 1265 (BM); *L. P. G. Smith* 284 (BM); Prainnha, Rio Pixuna, *Black* 47–2032 (BM); Téfe, *Black* 47–1572 (BM); Tapana, *Killip & Smith* 30356 (BM); Cachoeira do Tronco, Rio Cumina, *Sampaio* 4973 (BM); Utinga, near Belem, *Snethlage* 11 (B); Altar do Chao, *Traill* 1423 (K); Utinga, near Para, *Lutz* s.n. (BM).

Geographical range: Guiana and Amazonian Brazil to Peru.

Notes: 'Powdered leaves used on arms to protect from poisonous brew during preparation by witch doctors' (from a note on *Schultes & Cabrera* 15020).

107. Selaginella asperula Spring in Martius, *Fl. Bras.* **1** (2) : 127 (1840), in *Bull. Acad. r. Belg.* **10** : 230 (1843); *Mém. Acad. r. Sci. Lett. Belg.* **24** : 225 (1850); Baker, *Fern Allies* : 105 (1887); Alston in *Reprium Spec. nov. Regni veg.* **40** : 309 (1936): Knox in *Trans. bot. Soc. Edinb.* **35** : 251 (1950). Types from Brazil, Bahia: Barra, Panuré: *Spruce* 1317 (CGE, not seen).
Selaginella ovalis Baker in *J. Bot., Lond.* **21** : 143 (1883), *Fern Allies* : 48 (1887). Type from Brazil.

Specimens seen:
VENEZUELA. Amazonas: Cerro Duida, 150 m, *Steyermark* 57742 (BM); 945 m, *Tate* 890 (BM, NY); Esmeraldas, about 100 m, *Tate* 201 (BM, NY), 327 (NY); Capibara, about 100 m, *Holt & Gehringer* 283a (BM, NY); Yerba, 250 m, *Molina & Barkley* 18.v.194 (COL).
COLOMBIA. Amazonas: Rio Atabapo, 1 km W of Cacagual, *Maguire, Wurdack & Bunting* 36302 (BM). Caquetá: Florencia, *Perez Arbelaez* 621 (BM); Solano, 8 km SE of Tres Esquinas, on Rio Caquetá below mouth of Rio Orteguaza, 200 m, *Little* 9714 (COL). Meta: Gorge of R. Güejar, Sierra Macarena, 450 m, *Philipson* 2375 (BM); near Villavicencio, 480 m, *Alston* 7571 (BM); La Macarena, Sabanas de San Juan de Arama, 500 m, *Idrobo* 2619 (BM); La Macarena (Parte Sur), Rio Guayabero,

Sabanas de Arenisca, 235–700 m, *Barriga & Mejia* 17063 (AAU). Vaupés: near Piedra de Cocui, *Schultes & Lopez* 9522 (BM); Mesa la Lindosa, 4–600 m, *Idrobo & Schultes* 646 (BM, COL), 665, (BM, COL); Cerro Yapobodà, Rio Kuduyari, 450 m, *Schultes & Cabrera* 14216 (US), 14232 (COL, US), 20066 (US); Puerto Colombia, Rio Guainia, *c.* 250 m, *Schultes, Baker & Cabrera* 1794 (COL, US); San Felipe, Rio Negro, 185 m, *Schultes, Baker & Cabrera* 18125 (US); Cerro Isibukuri, Rio Kananari, 700 m, *Schultes & Cabrera* 13313 (COL, UC, US); Randal de Yurupari, *Schultes & Cabrera* 19725 (US); Savannah Goo-ran-hoo-dá, Mesa de Yambi, Rio Karurú, *c.* 300 m, *Schultes & Cabrera* 19162 (US); Cerro Kañendá Rio Kubiyú, 8–900 m, *Schultes & Cabrera* 18344 (US); Rio Paraná Pichuna, 215 m, *Schultes & Cabrera* 19912 (US); Cerro E-ree-eé-kö-mee-ö-kee, Rio Piraparaná, Rio Apaporis, *Schultes & Cabrera* 17493 (US); Jinogojé, Rio Apaporis, 215 m, *Schultes & Cabrera* 16589 (US).

PERU. Without precise locality: Chanchamajo, *Schunke* s.n. (BM). Junin: La Merced, 760 m, *Sandeman* 5024 (BM); Quimiri Bridge, La Merced, 800—1300 m, *Killip & Smith* 23833 (BM, NY); Colonia Perene, 680 m, *Killip & Smith* 24942 (BM); bank of Rio Perene, 1260 m, *Gascoyne-Cecil* 20 (BM), 670 m, *Gascoyne-Cecil* 82 (BM); Schunke Hacienda, above San Ramon, 1300–1700 m, *Schunke* A 250 (BM); San Ramon, 900–1300 m, *Killip & Smith* 24785 (NY). San Martin: Tingo Maria, 625–1100 m, *Allard* 20816 (BM), 20823 (BM), 21647 (BM), 21647a (BM); San Roque, 1350–1500 m, *L. Williams* 7415 (BM).

BOLIVIA. Tumupasa, 550 m, *R. Williams* 1396 (BM, NY).

BRAZIL. Amazonas: Manaos, *Spruce* s.n. (B, BM, CGE); *Solomon* s.n. (BM); *Schwacke* 188 (BM); *Tate* 47 (BM); *Killip & Smith* 30176 (BM); Campinarana, near Manaos, *Krukoff* 8015 (BM); Rio Mauhes, *Traill* 1416 (BM, K, type of *S. ovalis* Baker); Rio Xié, Upper Rio Negro, *Schultes & Lopez* 9202 (BM), 9218 (BM); Rio Taruma, *Froes* 24862 (BM, IAN); Taracua, Rio Uaupés, *Schultes & Pirés* 9031 (BM); Ipanoré, Rio Uaupés, *Schultes & Pirés* 9085 (BM), 9086 (BM); Taracuá, *Pirés* 910 (BM). Mucajai, Rio Branco, *Black & Magalhães* 12943 (BM, IAN); Rio Ayari, *Luetzelburg* 22505 (M); Tunuy, *Luetzelburg* 22944 (M); Tutica, Uaupés, *Luetzelburg* 23643 (M); Upper Rio Negro, *Weiss & Schmidt* s.n. (NY). Para: Posto dos Indios Caiabi, Rio Sao Manoel, *Pirés* 3861 (BM, IAN).

Geographical range: Amazonian Venezuela and Brazil south to Bolivia.

Notes: S. ovalis Baker was based on a prostrate, sterile branch of this species.

108. Selaginella fragilis A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 305 (1865), in *Mber. K. preuss. Akad. Wiss.* **1865** : 205 (1866); Alston in *Reprium Spec. nov. Regni veg.* **40** : 309 (1938). Type from Brazil, Amazonas: near Panure, Rio Uapès, *Spruce* 2533 (BM, CGE).

Selaginella vanheurckiana Spring in Van Heurck, *Pl. Nov.* : 28 (1870). Type as above.

Selaginella parkeri var. *vanheurckiana* (Spring) Baker in *J. Bot., Lond.* **23** : 120 (1885). Type as above.

Selaginella brachylepis Christ in *Bull. Herb. Boissier,* II, **1** : 74 (1901). Type from Peru.

Specimens seen:

VENEZUELA. Amazonas: near Salto de Huá, Serra Imeri, *Holt & Blake,* 504 (US); Rios Pacimoni-Yatua, Casiquiare, 110—130 m, *Maguire, Wurdack & Bunting* 37469 (BM).

COLOMBIA. Amazonas: Rio Miritiparaná, Cano Guacayá, 215 m, *Schultes & Cabrera* 15744 (UC). Amazonas-Vaupés: Rio Apaporis, Soratama, *Schultes & Cabrera* 16174 (COL). Antioquia: on Quebracha La Puya, east of Turbo, *c.* 75 m, *Haught* 4955 (COL). Putumayo: Umbria 325 m, *Klug* 1778 (BM). Vaupés: Cerra de Tipiaca, between Mitú and Javareté, *Schultes & Cabrera* 19303 (US); Cerro de Mitu, 250 m, *Schultes & Cabrera* 13930 (COL, US); below Teresita, Rio Papuri, *Schultes & Cabrera* 19476 (US); Cerro E-ree-eé-kö-mee-ö-kee, Rio Piraparaná, *Schultes & Cabrera* 17490 (US); Raudal Yayacopi, Rio Apaporis, 245 m, *Schultes & Cabrera* 16206 (US), 16907 (BM, US); Cachivera de Jirijirimo, Rio Apaporis, *Schultes* 12096 (BM); *Schultes & Cabrera* 12432 (COL, US); Soratama, between Rio Pacoa & Rio Kananari, 250 m, *Schultes & Cabrera* 12519 (US), 12778 (COL, US), 13617 (COL, US), 15969 (COL, US); *Garcia* 13954 (BM). Between Rio Ucayali and Huallaga, *Huber* s.n. (P, type of *S. brachylepis* Christ).

BRAZIL. Amazonas: type as above; Serra Curicuriarí, *Schultes & Lopez* 9838 (BM); Serra de São Gabriel, *Schultes & Lopez* 8760 (BM).

Geographical range: Amazonian Venezuela, Brazil and Colombia.

Notes: Perhaps not really distinct from *S. parkeri* (No. 109), from which it is distinguished by having branches with indeterminate growth which root at the apex.

109. Selaginella parkeri (Hook. & Grev.) Spring in *Bull. Acad. r. Belg.* **10** : 146 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 226 (1850), p.p. excl. syn. Klotzsch; Baker, *Fern Allies* : 104 (1887), excl. vars.; Knox in *Trans. bot. Soc. Edinb.*, **35** : 254 (1950). Type from Guyana, Demerara: *Parker* s.n. (K).

Lycopodium parkeri Hook. & Grev. in *Bot. Misc.* **2** : 388 (1831). Type as above.

Selaginella stellata sensu Spring in Martius, *Fl. Bras.* **1** (2) : 8 (1840), p.p., excl. fig. 203, non Fourn. (1872).

Lycopodium geniculatum sensu J. Smith in *J. Bot., Lond.* **1** : 203 (1842), non Presl (1825).

Selaginella lucidinervia Spring in *Bull. Acad. r. Belg.* **10** : 230 (1843). Syntypes from French Guiana.

Selaginella pedata Klotzsch in *Linnaea* **17** : 521 (1844). Type from Guyana.

Selaginella subarborescens Hook., *Second Cent. Ferns* : t.84 (1861). Type from Brazil.

Selaginella euryclada A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 304 (1865). Type from Brazil.

Selaginella eurycladоs A. Braun in *Mber. K. preuss. Acad. Wiss.* **1865** : 190, 203 (1866). Type as above.

Selaginella macroclada Baker in *J. Bot., Lond.* **22** : 23 (1884), *Fern Allies* : 61 (1887). Type from Guyana.

Selaginella parkeri var. *pedata* (Klotzsch) Baker in *J. Bot., Lond.* **23** : 120 (1885); *Fern Allies* : 104 (1887). Type from Guyana.

Selaginella flabellata sensu Wright in *Trans. Linn. Soc. Lond.* (Bot.) II, **6** : 88 (1901), non Spring (1838).

Specimens seen:

FRENCH GUIANA. Without exact locality: *Leprieur* 3 (P, type of *S. lucidinervia* Spring); *Aublet* s.n. (BM); Karonamy, *Sagot* 750 (BM, NY); near R Nousineri, *Leprieur* 176 (K).

SURINAM. Without exact locality: Pommier, Sara-creek, *Florschütz* 280 (BM); Makami Creek, *Lanjouw & Lindeman* 3020 (BM). Coronie: Boven Maratakka, *Gouggryp & Stabhel* 915 (U). Marowijne: Nassau Mts, *Lanjouw & Lindeman* 2250 (BM); Marowijne R, Nassau Mts, *Lanjouw & Lindeman* 2230 (BM); Nassau Mts, *Lanjouw & Lindeman* 2313 (BM). Nickerie: Timehri, Corantijn R, *Jenman* 376 (K); Corantijn R, *Jenman* s.n. (NY); *Hostmann* 880 (BM, U); *Dumontier* s.n. (U); Corantijn R, near Wonotono, *Stahel & Gouggryp* 2537 (U); *Rombouts* 72 (BM); Gran R, *Hulk* 253a (U); Nickerie R, *Tulleken* 482 (U, L), 362 (L), 389 (L); between Avanavero and Red Hill Falls, Kabalebo, *Florschütz* 2104 (BM). Saramacca: Saramacca R near Yambasigado, *Pulle* 434 (U); near Pakka-pakka, Saramacca R, *Florschütz* 1229 (BM); Tafelberg Creek, Saramacca R, *Maguire* 24104 (BM); Tafelberg, *Maguire* 24813 (BM); 425 m, *Maguire* 24696 (BM); between Pakka-pakka and Ebbatop, *Florschütz* 13922 (BM); Sarramacca R, *Maguire* 24142 (BM). Suriname: Surinam R, Goddo, *Tresling* 192 (U), 179 (U); Suhosa, Suriname R, *Lanjouw & Lindeman* 3375 (BM).

GUYANA. Without precise locality: type as above; *Schomburgk* 118 (BM, type collection of *S. pedata* Klotzch); *Appun* 802 (K, type of *S. macroclada* Baker); Mt Arisaru, *Guppy* 37 (BM); Macouria R, *Jenman* 2327 (BM, NY); *Appun* 728 (K); Rockstone, *Gleason* 687 (NY); *Hitchcock* 17320 (NY). Berbice: Sierra Acarai Region, 6 miles from Onoro, *Guppy* 244 (BM); 2nd plot ½ mile from camp 1, *Guppy* 260 (BM); 1st field by mission, *Guppy* 193 (BM); behind Mission, *Guppy* 235 (BM). Demerara: *Anderson* 244 (BM); *Jenman* s.n. (NY); Great Falls, Demerara R, *Jenman* s.n. (NY); between Demerara and Berbice R, *De La Cruz* 1593 (NY). Essequibo: near Burroburro Creek, *Sandwith* 1090 (BM); *Quelch & McConnell* 115 (K); Kuyuwini R, *A. C. Smith* 2552 (BM); Akarai Mts, 600–800 m, *A. C. Smith* 2998 (BM); Calalebo, *im Thurn* s.n. (K); Pomeroon R, *Jenman* s.n. (NY); Marlissa crossline, Berbice to Rupununi Cattle Trail, *Abraham* 251 (NY); Moraballi Creek, Bartica, *Richards* 14 (BM, K); Baracara, Mazaruni, *Barkly* s.n. (BM); Takutu Creek, to Puruni R, Mazaruni, *Fanshawe* 2121 (BM); Tumutumari, *Gleason* 91 (NY), 98 (K, NY), 99 (NY), 458 (NY); *Jenman* s.n. (NY); Tiger Creek, Tumutumari, *Tutin* 543 (BM); Omia Creek Essequibo R, *Jenman* s.n. (NY); Mazaruni station, *Tutin* 178 (BM); Potaro R, *Jenman* s.n. (NY); Junction of Mazuruni and Cuyuni R, *Graham* 314 (NY); Kurupung, Upper Mazaruni R, *Leng* 175 (NY), 196 (NY); along cattle-trail to Kurupukari, *Beccari* s.n. (FI).

VENEZUELA. Amazonas: Yavita, 128 m, *L. Williams* 14058 (BM). Bolivar: Mt Duida, 230 m, *Tate* 1007 (NY); Rio Torono, above junction with Rio Paragua, 280 m, *Killip* 37400 (BM). Rio Paragua: Salto de Auraima, 275 m, *Killip* 37342 (BM).

COLOMBIA. Amazonas: Rio Miritiparaná, 210 m, *Schultes & Cabrera* 16470 (BM, US); Rio

Miritiparaná, Cano Guacaya, 215 m, *Schultes & Cabrera* 15719 (UC). Caquetá: Florencia, *Perez Arbelaez* 630 (BM), 667 (BM); Morelia, 350 m, *v. Sneidern* A1263 (S). Putumayo: Umbria, 325 m, *Klug* 1711 (BM, NY), 1788 (BM, NY); Solano, 8 km SE of Tres Esquinas, on Rio Caqueta below mouth of Rio Orteguaza, 200 m, *Little* 9520 (COL). Vaupés: Mitu, 250 m, *Schultes & Cabrera* 13962 (COL, US), 13966 (US); Caño Teemeeña, Rio Piraparaná, *Schultes & Cabrera* 17186 (COL, US), 17416 (COL, US); Caño Peritomé, below Randal Yayacopi, Rio Apaporis, *c.* 230 m, *Schultes & Cabrera* 15514 (US); Soratama between Rio Pacoa and Rio Kananari, 250 m, *Schultes & Cabrera* 12865 (US), 16078 (US); Randal de Jerijerimo, *Schultes* 12097 (BM); Cerro Isibukuri, 250–700 m, *Schultes & Cabrera* 13310 (COL, UC, US), 13329 (US), 14450A (US); Soratama, Rio Apaporis, 250 m, *Schultes & Cabrera* 12779 (COL, US), 16079 (US).

BRAZIL. Without exact locality: *Glaziou* 10211 (C, K); *Glaziou* 16647 (BM). Amazonas: Manaos, *Ule* 5311 (K); *Schwacke* s.n. (BM); W bank of Manhos R, *Traill* 1419 (K); Manaos, *Luetzelburg* 22014 (M); Camanaos, Rio Negros, *Leutzelburg* 20356 (M); Janarete, Papori, *Luetzelburg* 23001 (M); S Maria, Papori, *Luetzelburg* 22797 (M); 80 km N of Manaus on side trail, *J.B.S.* 189 (BM); Panure, Rio Uaupés, *Spruce* 2540 (BM, CGE, type of *S. euryclada* A. Braun); Serra Baraö, Igrapé da Chuva, Taracuá, Rio Uaupés, *Schultes & Pirés* 9056 (BM); Rio Negro, 25 km NW of Manaus, 50 m, *Conant* 1161 (BM); Reserva Ducke, km 26, Manaus-Hacoatiara Road, *Conant* 891 (BM). Para: Rio Cuminá, *Sampaio* 509 (BM); R Aripecuru, *Spruce* s.n. (BM, CGE).

Geographical range: Colombia, The Guianas, Amazonian Venezuela and Brazil.

Notes: A species characterised by having 2 or 3 strobili at the ends of its branches. This species sometimes develops a kind of witch's broom, whose cause is unknown. *Killip* 37400 (BM) and *im Thurn* s.n. (K) are examples. *S. macroclada* Baker (*Appun* 802) is probably a prostrate, sterile branch of this species. *S. pedata* Klotzsch is usually smaller in leaf than *S. parkeri* but is otherwise identical. Alston maintained *S. subarborescens* Hook. on leaf shape and margin characters; also growth habit, suggesting it is broader. Somers (1978) found little difference except the lateral leaves lacked an upper auricle and the megaspores showed narrow high muri. We find the characters mixed and grade into a cline and therefore consider them as one taxon. It is a group that requires further study.

110. Selaginella arthritica Alston in *Archo bot.* **11** : 43 (1935). Type from Costa Rica, *Cufodontis* 218 (BM).

Selaginella conduplicata Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 229 (1850), p.p. quoad pl. Colomb. Syntypes from Brazil, Colombia and French Guiana.

Selaginella geniculata sensu Baker, *Fern Allies* : 105 (1887), p.p. quoad pl. centrali-americana.

Selaginella geniculata var. *conduplicata* (Spring) A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 303 (1865), p.p. quoad pl. Colomb. Type as above.

Specimens seen:

COLOMBIA. Antioquia: Villa Arteaga, Mutatá, Uraba, 30–60 m, *Schultes & Cabrera* 18662 (US); Turbo, Golfo de Uraba, *Schott* 2 (NY); Rio Ampurrumiado, 200 m, *Gutierrez & Barkley* 17c213 (BM); Guapa, S of Turbo 100 m, *Haught* 4659 (BM); Quebrada Congo, E of Guapa, 150 m, *Haught* 4664 (BM, COL). Chocó: Rio Nuqui, 50 m, *Haught* 5460 (BM, COL).

ECUADOR. Santiago-Zamora: near Mendez, 525–750 m, *Camp* E 893 (BM, NY).

Geographical range: Colombia and south-east Ecuador, at low elevations.

Notes: Schultes & Cabrera 18662 from Antioquia is a large form.

111. Selaginella geniculata (C. Presl) Spring in *Bull. Acad. r. Belg.* **10** : 230 (1843); C. Presl, *Bot. Bemerk.* : 151 (1844); Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 227 (1850); A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 313 (1865); in *Mber. K. preuss. Akad. Wiss.* **1865** : 206 (1866); Baker, *Fern Allies* : 105 (1887), p.p.; Alston in *J. Bot., Lond.* **72** : 226 (1934); Knox in *Trans. bot. Soc. Edinb.* **35** : 285 (1950). Type from Peru or Ecuador (see *Notes*).

Lycopodium geniculatum C. Presl, *Rel. Haenk* : 80 (1825); Spreng., *Syst. Veg.* **4** : 19 (1827). Type as above.

Selaginella ferruminata Spring in *Bull. Acad. r. Belg.* **10** : 231 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 250 (1850). Type from Peru.

Selaginella elongata Klotzsch in *Linnaea* **18** : 522 (1844). Type probably from Peru.

Selaginella geniculata var. *elongata* (Klotzsch) A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 303 (1865). Type as above.

Selaginella geniculata subsp. *elongata* (Klotzsch) Hieron. in Engl. & Prantl, *Nat. Pflanzenf.* **1** (4) : 712 (1901). Type as above.

Selaginella nodosa C. Presl, *Bot. Bemerk.* : 50 (1844); in *Abh. K. Böhm. Ges. Wiss.* V, **3** : 580 (1844). Type from Peru.

Lycopodium flabellatum sensu Kunze in *Linnaea* **9** : 9 (1835), non L. (1753).

Specimens seen:

COLOMBIA. Antioquia: Quebrada San Julian, near Argelia, 1800 m, *Ewan* 15780 (BM). Caldas: La Selva, Pueblo Rice, 1500 m, *v. Sneidern* 5490 (S); above Calarca, 1900 m, *Alston* 7778 (BM). Caqueta: Florencia, *Perez Arbelaez* 626 (BM). Cauca: W of Tambo, 1100 m, *Haught* 5219 (BM); I. of Gorgona, *Barclay* 906 (BM); Teta, *Lehmann* BT 919 (NY). Chocó: Bay of Chocó, *Seemann* s.n. (BM); Rio Naqui, 300 m *Haught* 5495 (BM). Cundinamarca: near Bogota, 1000 m, *Triana* s.n. (BM). Nariño: between Ricuarte & Diviso, *Espinosa* 2945 (BM); below Ricuarte, 1200 m, *Alston* 8449 (BM); near Altaquer, 1000 m, *Lehmann* 86 (BM); Rio Puelmambi, 1540 m, *Ewan* 16038 (BM). Putumayo: Mocoa, 550–730 m, *Schultes & Cabrera* 19046 (COL, US); between Urcusique and Mocoa, *Ewan* 16793 (BM); Rio Ticuanayoy, 1100 m, *Ewan* 16805 (BM). Valle del Cauca: Quermal, Dagua Valley, *Perez Arbelaez* 3206 (BM); 1300 m, *Alston* 7799 (BM); La Cubre, 1600–1800 m, *Killip* 5673 (NY).

ECUADOR. Without precise locality, *Jameson* 210 (BM), 74 (NY); Andium Quitensium temperate forest region, *Jameson* 4 (NY), 60 (NY). Chimborozo: Hacienda de Licay near Huigra, *Rose* 22597 (NY). Guayas: near Quillallpa, 150 m, *Fagerlind & Wibom* 682 bis (S); near Bucay, 305–393 m, *Camp* E3846 (BM); near Guayaguil, *Jameson* 401 (BM). Los Rios: Hacienda Clementina on Rio Pita, *Asplund* 5501 (S). Napo-Pastaza: Bimbino, banks of Rio Pacuno, 10 hrs W of confluence with Rio Napo at Bimbino, 300 m, *Whitmore* 786 (BM); Archidona, *Jameson* 767 (BM); between Tena and Archidona, *Asplund* 9452 (S); Tena, *Asplund* 9420 (S); Vicinity of Ventura, *Rose* 23969 (NY). Pichincha: by Rio Toachi, near the confluence with Rio Pilaton, 915 m, *Bell* 218 (BM), 286 (BM); Santo Domingo de los Colorados, *Fagerlind & Wibom* 1636 (S); San Carlos des los Colorados, *Fagerlind & Wibom* 1636 (S); Hacienda Solento, near Santa Rosa, Canton Pajili. 1000 m, *Mexia* 6735 (BM). Santiago-Zamora: near Mendez, 325–750 m, *Camp* E893 (BM); below Zamora, 900 m, *Camp* E49 (BM); between Rio Sabanilla & Cannilones Tambo, 1370–2135 m, *Camp* E65 (BM).

PERU. Huanuco: Tingo Maria, *Asplund* 12358 (BM). Junin; San Nicolas, Pichis Trail, 1100 m, *Killip & Smith* 26022 (BM), NY); Pangoa, *Matthews* 1083, (BM, type of *S. ferruminata* Spring). Loreto: between Yurimaguas and Balsapuerto, 135–150 m, *Killip & Smith* 28250 (BM, NY); near Tarapoto, *Spruce* 4624 (BM, CGE). San Martin: Las Cueras de los pavos, Tingo Maria, 625–1100 m, *Allard* 20532 (BM); Juan Jui, Alto Rio Huallaga, 400 m, *Klug* 3831 (BM).

Geographical range: Colombia, Ecuador and Peru to 12°S.

Notes: Presl's type in the National Museum at Praha, is localised 'Luzon', but it must have been from Peru or Ecuador. *Killip & Smith* 14830 and 14843, both from Santander Colombia, have auricles on the lateral leaves, and a medium leaf size and shape similar to *S. parkeri* (No. 109).

112. Selaginella dasyloma Alston in *J. Bot., Lond.* **72** : 228 (1934). Type from Colombia, Huila: Sombrerillo, *André* 343 (K, holotype; BM, NY, isotypes).

Specimens seen:

COLOMBIA. Huila: type as above.

ECUADOR. Unlocalised, in Cauca or Tolima, 600–1700 m, *Alexander* s.n. (BM, NY). Santiago-Zamora: between Hacienda Chontal and Santa Elena, 1020–1380 m, *Camp* E768 (BM).

Geographical range: Colombia and Ecuador.

Notes: This species may be distinguished from all other prostrate, articulate species by its large, obtuse, median leaves.

113. Selaginella anaclasta Alston ex Crabbe & Jermy in *Am. Fern J.* **63** : 135 (1973). Type from Venezuela, Amazonas: Cerro de la Neblina, Rio Yatua, *Maguire, Wurdack & Bunting* 37063 (US; BM, fragment).

Specimens seen:
VENEZUELA. Amazonas: type as above.

Geographical range: Confined to Venezuela.

Notes: The multicellular teeth at the base of its leaves make this one of the most distinct species in the genus.

114. Selaginella kunzeana A. Braun in *Annl Sci. nat.* (Bot). V, **3** : 296 (1865); Baker, *Fern Allies* : 62 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 291 (1950). Type from Peru, Huanuco: Pampayaco, *Poeppig* 195 (BM, P).

Lycopodium poeppigianum sensu Kunze in *Linnaea* **9** : 11 (1834), non Hook. & Grev. (1831).

Specimens seen:
VENEZUELA. Amazonas: Great Rapids of the Orinoco, Raudal de Atures 10 km S of Pto Ayacucho, 100–120 m, *Maguire, Wurdack & Bunting* 36139 (BM).
COLOMBIA. Antioquia: Rio Chiado, S of Turbo, 80 m, *Haught* 4635 (BM, COl); carretera de Medellin a Turbo, *Cabrera* 27 (COL); zona Cauchera de Villa Arteaga, *Cabrera* 54 (COL). Boyaca: Muzo Mines, 700 m, *Lindig* 1513 (BM). Caldas: Santa Cecilia Tatamá, 800 m, *v. Sneidern* 5062 (S). Caqueta: Florencia, *Perez Arbelaez* 622a (BM). Cauca: 'La Gallera' Micay Valley, 1400–1500 m, *Killip* 7676 (NY, US), 7852 (NY, US). Choco: Rio Nugui, 50 m, *Haught* 5461 (BM, COL); La Equis, *c.* 200 m, *Molina & Barkley* 19 Ch 085 (COL). Cundinamarca: La Palma, *Triana* s.n. (BM); 1150–1400 m, *Garcia* 12376 (BM), 12418 (BM); between La Palma and Pacho, 1100 m, *Haught* 6092 (BM, COL); Pandi, *Herb. Nac. Colombeano* 492 (US); Toraima, *Lindig* 1510 (P); between Cachipay and La Esperanza, *Little* 9462 (COL). Magdalena: above Onacu, 915 m, Santa Marta, *Smith* 2468 (BM, NY, US); Manaure, between Cordillera Central and Santa Marta, 975 m, *Foster* 1585 (COL). Valle del Cauca: valley of Rio Digua, 950 m, *Alston* 7805 (BM).
ECUADOR. Chimborozo: without further location, *Spruce* 5675 (BM, CGE). Guayas: Salango, *Barclay* 633 (BM); Teresita, W of Bucay, 270 m, *Hitchcock* 20423 (US). Los Rios: near Quevedo, Canton Vinces, 50 m, *Mexia* 6618 (BM). Manabi: El Recreo, *Eggers* 14878 (P, S). Napo-Pastaza: between Baños & Mera, 4–500 m, *Mexia* 6974 (BM); Cashurco, *Asplund* 19363 (S). Santiago-Zamora: Rio Pante, W of Mendez, 580 m, *Camp* E1458 (BM). Tungurahua: between Baños and Cashurco, 1300—1800 m, *Hitchcock* 21897 (NY, US).
PERU. Ayachucho: Estrella, between Huanta and Rio Apurimac, 500 m, *Killip & Smith* 22663 (BM, NY). Huanuco: type as above; Tingo Maria, *Asplund* 12140 (BM); Cueva de las Pavas, near Tingo Maria, 500–600 m, *Ferreyra* 2892 (BM); Cuchero, *Dombey* s.n. (P); Hacienda Mercedes, Churubamba, 1870 m, *Mexia* 8197 (BM); Casapi, *Matthews* 1760 (BM). Loreto: Monte Campana, near Tarapoto, *Spruce* 4630 (BM, CGE, NY); between Tingo Maria and Pucallpa, 1400–1500 m, *Ferreyra* 2218 (BM). San Martin: Tingo Maria, 625–1100 m, *Allard* 20361 (BM); Carpish, near Tingo Maria, *Gascoyne-Cecil* 105 (BM); Mariscal caceres, 60 km NE of Tingo Maria, 'Divisoria' pass through Cerro Azul on Tingo Maria-Pucallpa road, 1500 m, *R. & A. Tryon* 5272 (BM).

Geographical range: Mexico southwards to Peru.

115. Selaginella lingulata Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 224 (1850); Baker, *Fern Allies* : 64 (1887), p.p. excel. syn. A. Braun; Knox in *Trans. bot. Soc. Edinb.* **35** : 285 (1950). Type from Ecuador, Pinchincha: *Jameson* s.n. (BM, K).

Selaginella intacta Baker in *J. Bot., Lond.* **21** : 335 (1883), *Fern Allies* : 60 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 285 (1950). Type from Ecuador.

Selaginella lindigii A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 297 (1865); Baker, *Fern Allies* : 65 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 285 (1950). Lectotype from Ecuador.

Specimens seen:
COLOMBIA. Antioquia: near Santa Elena, 2300—2500 m, *Gutiérrez & Barkley* 17c024 (BM). Chocó: Rio Nuqui, 50 m, *Haught* 5459 (COL). Cundinamarca: El Salto de Tequendama, near Bogota, 2550 m, *Triana* 696 (BM); *Lindig* 1507 (BM); *Ariste-Joseph* s.n. (US), A 392 (US); *Holton s.n.* (K); *Alston* 7415 (BM); *Hermanos* 17 (NY); 2300 m, *Cuatrecasas* 198 (COL); Falls of Rio Bogota, vicinity of El Salto, 2470–2530 m, *Little* 7896 (COL); Salto de Tequendama, 2100 m, *Alston* 7415 (BM); Barroblanco, *André* 1483 (K), 1388 (K). Putumayo: between Lake Cocha and Santiago, 2350 m, *Alston* 8344 (BM); near Lake Cocha, 2700 m, *Alston* 8321 (BM). Tolima: Quindio Road, 3000 m, *Alston* 7777 (BM); Quebrada Peralis, Quindiva Road, 2600 m, *Alston* 7751 (BM). Vallee del Cauca: Cordoba, Dagua Valley, 80–100 m, *Killig* 5047 (US).
ECUADOR. Without precise locality: *Spruce* 4798 (BM, CGE, NY; lectotype of *S. lindigii* A.Br.); between Río Gamolotal and Río Norcay, 1095–1370 m, *Steyermark* 52854 (BM); Andes Quitense, *Spruce* 5603 (CGE, NY). Carchi: between El Pun and Puenta Chingual, *Asplund* 16982 (S). Guyas: Guayaquil, *Jameson* s.n. (BM); San Nicolo, *Sodiro* 71 (K, type of *S. intacta* Baker). Napo-Pastaza: Baeza, 2000—2200 m, *Balslev & Madsen* 10318 (BM). Pichincha : type as above; Salvador, 2440 m, *Bell* 667 (BM); Aloag, El Corazon, 2865 m, *Wiggins* 10694 (BM); Nono Gualea, *Sodiro* s.n. (NY); woods on the western side of Pichincha, *Jameson* 43 (K); Corazon, *Sodiro* s.n. (K). Santiago-Zamora: between Campanas and Arenillas, along Rio Tinta, 10 leagues SE of El Pan, 2195 m, *Steyermark* 53617 (BM).
PERU. Without exact locality: Pichis Highway, *Bradley* 66666 (US). Huanuco: near Puente Durand, between Huanuco and Tingo Maria, 1500–1600m, *Ferreyra* 2937 (BM). Junin: Chanchamayo Valley, *Schunke* 788 (US); Schunke Hacienda, above San Ramon, 1800m, *Schunke* A249 (US); 1300–1700m, *Schunke* A251 (US); Pichis Trail, San Nicolas, c. 1100m, *Killip & Smith* 26056 (BM).
BOLIVIA. Without exact locality: Songo, *Bang* 909 (US). La Paz: Ticunhuaya, 1525 m, *Tate* 1076 (US).

Geographical range: Colombia south to Bolivia.

Notes: Somers (1978) considered the type of this species to be atypical, having nearly elliptical and widely spaced lateral leaves which could be indicative of shade growth, which grades into the form hitherto called *S. lindigii* A. Braun. Similarly Somers (l.c) regarded the type of Baker's *S. intacta* to be an extremely depauperate form of *S. lingulata*, often confused with *S. atirrensis* (No. 120), but lacking the multicellular cilia of that taxon. *Archer* 1517, from Colombia, is typical, having the auricles of the median leaf somewhat unequal, and with scant cilia on the axillary leaf bases.

116. Selaginella articulata (Kunze) Spring in *Flora, Jena* **21** : 182 (1838), in *Annls Sci. nat.* (Bot.) II, **11** : 228 (1839), in *Bull. Acad. r. Belg.* **10** : 229 (1843), *Mém. Acad. r. Sci. Lett. Belg.* **24** : 211 (1850); Baker, *Fern Allies* : 82 (1887); Knox in *Trans. bot. Soc. Edinb.* **35** : 283 (1950). Type from Peru, Loreto: Maynas Alto, *Poeppig* s.n. (K, P).
Lycopodium articulatum Kunze in *Linnaea* **9** : 10 (1835), *Farrnkr.* **1** : 243 (1847). Type as above.

Specimens seen:
COLOMBIA. Putumayo: above Mocoa, 600 m, *Ewan* 16710 (BM).
ECUADOR. Napo-Pastaza: Archedonia, *Jameson* 714 (BM); Mera, *Asplund* 18781 (S); near Tena, 400 m, *Mexia* 7219 (BM); between Puyo and Canelos, 325–375 m, *Mexia* 6842 (BM); near Puyo, *Fagerlind & Wibom* 1185 (S); Mera, 1200 m, *Øllgaard & Balslev* 9096 (AAU, BM); near Hacienda Ortiz, 18 km from Puyo on road to Tena, 1100 m, *Øllgaard & Balslev* 9264 (AAU, BM).
PERU. Loreto: type as above; Monte Campana, near Tarapoto, *Spruce* 4627 (BM, CGE, NY).

Geographical range: Colombia, Ecuador and Peru.

Notes: Distinguished from the other two pubescent articulate species (Nos. 104 and 105) in having rather close, spreading, obtuse leaves on the main stem. *S. sericea* (No. 128) is a very similar species, but the stems are always glabrous and the lateral leaves have two auricles.

117. Selaginella valida Alston in *J. Bot., Lond.* **70** : 281 (1932). Type from Brazil, São Paulo: S José do Barreiro, *Hoehne & Gehrt* 17698 (BM).

Specimens seen:
BRAZIL. São Paulo: Santos, *Mosen* 3812 (P); type as above.

Geographical range: So far recorded only in São Paulo.

118. Selaginella calceolata Jermy & Rankin **sp. nov.** (Figs 17 & 18)
Selaginella arenaria Baker in *J. Bot., Lond.* **21** : 82 (1883), p.p. non spec. in herb. Kew.
Planta caulibus prostratis ramis ascendentibus, foliis intermediis calceolatis auricula exteriore magna distincta.

Caules prostrati articulati pallidi straminei; rhizophoris dorsaliter exorientibus; ramis paucis, primariis 3–6 cm longis, alternis, saepe suberectis, ultimis 1–2 cm longis, patentibus, *Folia* ubique heteromorpha; *folia lateralia* 1·8–2·2 mm longa, 0·8–1·1 mm lata, oblongo-elliptica vel oblongo-lanceolata, apice obtuso vel subacuto, semifacie superiore denticulata, basi rotundata, semifacie inferiore basi truncata apicem versus denticulata, aliter integra; *folia axillaria* 1·8–2·0 mm longa, *c.* 0·7 mm lata, oblongo-elliptica, denticulata, apice rotundato vel late obtuso, basi plus minusve cuneata; *folia intermedia* 1·5–1·8 mm longa, 0·5–0·6 mm lata, adpressa, imbricata, calceolata, auricula magna exteriore calceum faciente, apice acuto vel subacuto, integri, margine inconspicuo. *Strobili* 1–2 mm longi, basi feminei, supra masculi; *megasporophylla c.* 1·5 mm longa, 0·7 mm lata, late ovata, apice denticulato, acuminato vel acuto; *megasporae* reticulatae; *microsporophylla* 0·8 mm longa, 0·4 mm lata, megasporophyllo similia sed manifestius carinata; *microsporae* non visae.

Typus: Colombia: Puerto Lopez, Intendencia del Meta, in ripa humida umbrosa, 240 m, 27 July 1944, *E.L. & R.R. Little* 8241 (COL, holotype; BM, US, isotypes).

Other specimens seen:
COLOMBIA. Boyaca: Orucué, Los Llanos, Rio Meta, 140 m, *Cuatrecasas & Barriga* 4389 (COL).
BRAZIL. Amazonas: on Rio Vaupés at Panuré, *Spruce* 2861 (BM).

Geographical range: Eastern Colombia to western Brazil.

Notes: Spruce's gathering was mixed, and only the specimen at Kew agrees with Baker's description of *S. arenaria* (No. 78), thus necessitating the description of this species. We are grateful to Paul Somers for drawing attention to this situation.

119. Selaginella marginata (Humb. & Bonpl.) Spring in *Flora, Jena,* **21** : 194 (1838), in Martius, *Fl. Bras.* **1** (2) : 117 (1840), ex Decne in *Arch. Mus.* **2** : 192 (1841–42), in *Bull. Acad. r. Belg.* **10** : 229 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 211 (1850), p.p. excl. loc. mexicanis; A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 291 (1865); Baker, *Fern Allies* : 61 (1887). Type from Venezuela, Apure: mouth of R Meta, *Humboldt* s.n. (B).
Lycopodium marginatum Humb. & Bonpl. ex Willd., *Spec. Pl.* **5** : 41 (1810); Kunth, *Nov. Gen. Spec.,* **1** : 391 (1816), *Syn. Pl.* **1** : 96 (1822); Sprengel, *Syst. Veg.* **4** : 18 (1827). Type as above.
Selaginella excurrens Spring in Martius, *Fl. Bras.* **1** (2) : 128 (1840). Type from Brazil.
Selaginella marginata subsp. *distorta* Spring in *Flora, Jena* **21** : 196 (1838). Type from Brazil.
Selaginella marginata var. *minor* Spring *l.c.* Type from Brazil.
Selaginella distorta (Spring) Spring in *Bull. Acad. r. Belg.* **10** : 229 (1843).
Selaginella distorta var. *minor* (Spring) Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 213 (1850).
Selaginella distorta var. *major* Baker in *J. Bot., Lond.* **21** : 335 (1883). Type from Brazil.
Selaginella chromatophylla Silveira in *Bolm Comm. geogr. geol. Minas Geraes* **5** : 124 (1898) and vars. Types from Brazil.
Selaginella urbanii Hieron. in Engl. & Prantl, *Nat. Pflanzenf.* **1** (4) : 709 (1901). Type from Brazil.
Selaginella moseni Hieron. *l.c.* : 709. Type from Brazil.
Selaginella burchellii Hieron. *l.c.* : 709. Type from Brazil.

Fig. 17 *Selaginella calceolata* Jermy & Rankin: Type specimen, *E.L. & R.R. Little* 8241 (COL).

Fig. 18 *Selaginella calceolata* Jermy & Rankin: **A.** Close-up of lateral (*l*) and axillary (*a*) leaves, × 25. **B.** Close-up of median leaf, × 56. Both from *E.L. & R.R. Little* 8241.

Selaginella excurrens var. *glazioviana* Hieron. ex Rosenstock in *Hedwigia* **46** : 166 (1907). Type from Brazil.

Selaginella breuensis Silveira in *Fl. Serras Mineiras* : 79 (1908). Type from Brazil.

Selaginella herteri Hieron. in *Reprium Spec. nov. Regni veg.* **13** : 421 (1914). Type from Uruguay.

Selaginella caracensis Goebel in *Flora, Jena* **108** : 316 (1915). Type from Brazil.

Selaginella ypirangensis Hieron. ex Herter in *Beih. bot. Zbl.* **39** : 253 (1922). Type from Brazil.

Selaginella ypirangensis var. *riograndensis* Herter *l.c.* : 256. Type from Brazil.

Selaginella wielewskii Hieron. ex Rosenstock in *Hedwigia* **43** : 234 (1904). Type from Brazil.

Specimens seen:

VENEZUELA. Without exact locality: *Grosse* s.n. (BM). Apure: type as above. Aragua: San Matos, *Famayo* 633 (BM). Guarico: between San Juan de los Morros and Parapara, 400 m, *Alston* 5997 (BM), 6004 (BM).

BOLIVIA. Santa Cruz: S Cruz, 422 m, *Tutin* 1549 (BM); 460 m, *Brooke* 5844 (BM).

BRAZIL. Without exact locality: *Glaziou* 15802 (C, P), 22646 (C), 7355 (BM, C), 7969 (C), 15803 (C), 12296 (BM, C); *Langsdorf* s.n. (K); *Sellow* s.n. (K); *Burchell* 8724 (K); *Dusen* 3726 (BM). Bahia: *Blanchet* s.n. (M). Goias: 25 km N of Brasilia, 950 m, *Irwin, Souza & Reis dos Santos* 11282 (BM). Maranhão. Ilha dos Botes, Carolina Rio Tocantins, *Pirés & Black* 2037 (BM). Mato Grosso: Corumbá, *Robert* 728 (BM); *Hoehne* 45 (BM); *Rasteira* s.n. (BM); Sierra de Chapada, *Moore* 85 (BM). Minas Gerais: without further locality; *Glaziou* 20116 (C); *Claussen* s.n. (P), *St Hilaire* 272 (P); Conselheira Matta-Rodeador, *Brade* 13961 (BM); Campanha, *Schreiner* s.n. (BM); Rio Grande do Sus, Caldas, *Mosen* s.n. (BM); Caldas, *Mosen* 2018 (P), 2019 (C, P), 2020 (P), 2021 (C, P), 2023 (C); Santa Barbara do Matto Dentro, *Hoehne* 5004 (BM); Casa de Pedra, Tiradentes, *Silveira* 160 (BM); Serra do Cipo, *Silveira* 395 (BM); Serra do Papagaio, *Silveira* 152 (BM); Palmeiras, *Lindman* A 2499 (NY); Cuyaba, *Lindman* A 2347 (K). Parana: *Schwacke* s.n. (BM); between Cuntiba and Butiatuba, *Schwacke* Coll. II No. 37 (BM), 2706 (BM, P); Serra do Mar, Ypiranga, *Dusén* 3726 (BM, P); Lucena, *Wielewski* 7 (NY);

Rio Negro, *Annies* 93 (NY); Serrimba, *Dusén* 15188 (BM); Serra do Mar, Banhado, *Dusén* 14465 (BM); Curitiba, *Augley & Mattos* 3831 (UC). Piaui: *Netto* 80 (BM). Rio de Janeiro: without further locality, *Raben* s.n. (BM, C), Santa Magdalena Pedra das Flores, *Lima & Brade* 13190 (BM); Serra dos Orgaõs, 1000 m, *Brade* 16811 (BM); Sto Antonio, *Glaziou* 7355 (BM). Rio Grande du Sol: Villa Germania, *Jürgens* L 23 (BM, NY); *Jürgens & Stier* 310 (BM); Cachoeira, *Lindman* A 1153 (BM); Nova Wuertemberg, *Jürgens & Stier* 311 (BM); Taquara, Caracol, *Dutra* 1612 (BM); S Antonio da Patrulha, *Dutra* 134 (BM); Bomjesus, *Dutra* 235 (BM), 1608 (BM); S Francisco de Paula, *Rambo* 44799 (BM), 46312 (BM), 45638 (BM); Aparados da Rocinha near Bom Jesus, *Rambo* 45363 (BM); Toca do Tigre near Itapoan, *Rambo* 48844 (BM). Santa Catarina: Lages, *Rambo* 49548 (BM); *Spannagel* 103 (NY), 235 (NY), 417 (BM); Vaccão Gordão, Lages, *Spannagel* 45 (NY). São Paulo: Campos do Jordaõ, *Porto* 3114 (BM); 1600 m, *Leite* 3658 (BM); Lorena, *Luederwaldt* s.n. (BM).

Geographical range: Mexico, southwards to Uruguay and northern Argentina.

120. Selaginella atirrensis Hieron. in Engl. & Prantl, *Nat. Pflanzenf.* **1** (4) : 711 (1901); Knox in *Trans. bot. Soc. Edinb.* **35** : 290 (1950). Type from Costa Rica, Cartago: near Atirro, 650 m, *Donn Smith* 5103 (NY, US).

Selaginella intacta sensu auct., non Baker (1883).

Specimens seen:

COLOMBIA. Cauca: Cordillera occidental, 1600 m, *Bischler* 1497 (COL). Chocó: bank of Rio San Juan, near Andagoya, *c.* 60 m, *Killip* 35379 (COL); between La Oveja and Quibdo, *Archer* 1666 (BM). Narino: *Lehmann* 88 (BM). Valle del Cauca: Rio Calima, between Pailon and El Coco, 50 m, *Cuatrecasas* 21244 (BM); km 99 on Cali-Buenaventura Highway, *c.* 200 m, *Haught* 5319 (BM, COL); Cordoba, Dagua Valley, *Killip* 5048 (US), 5032 (US).

PERU. Junin: Chanchamayo valley, 1500 m, *Schunke* 229 (BM); Schunke Hacienda, above San Ramon, 1300–1700 m, *Schunke* A251 (BM); 1800 m, *Schunke* A249 (BM).

Geographical range: Costa Rica south to Colombia.

121. Selaginella kraussiana (Kunze) A. Braun, *Appl. Ind. Sem. Hort. Berol.* : 22 (1860); Baker, *Fern Allies* : 65 (1887). Type from South Africa: Zitzikamma District, *Kraus Marks* s.n. (? B).

Lycopodium kraussianum Kunze in *Linnaea* **18** : 114 (1844). Type as above.

Selaginella hortensis Mett., *Fil. Hort. Lips.* : 125 (1856). Type ex hort. Lips.

Selaginella canescens Fée, *Crypt. Brés.* **2** : 99 (1873); Alston in *Reprium Spec. nov. Regni Veg.* **40** : 318 (1936). Type from Brazil.

Selaginella denticulata Hort.; *Jl R. hort. Soc.* **8** : 35, 123 (1887), non (L.) Link (1841). Type from Canarias.

Specimens seen:

BRAZIL. Rio de Janeiro: *Glaziou* 4489 (C, K; type of *S. canescens* Fée), 12297 (C, K). Rio Grande do Sul: S Cruz, *Jurgens* L 35 (BM). Santa Catarina: Joinville, *Schmalz* 149 (BM, NY); Cantareira, *Usteri* s.n. (BM).

Geographical range: Native to Africa and Macaronesia but escaped from cultivation or accidentally introduced in the New World from Virginia to Chile.

Notes: This was described by Fée as an endemic species, *S. canescens,* which, as far as we can see, is conspecific with *S. kraussiana.* The general assumption is that it has been introduced in South America, but it is conceivable that it is native. It is distinct from other articulate species, all of which are confined to the neotropics.

122. Selaginella asplundii Alston ex Crabbe & Jermy in *Fern Gaz.* **11** : 257 (1976). Types from Peru, Huanuco: Carpish, 2700 m, *Asplund* 12822 (S, holotype; BM, isotype).

Specimens seen:

COLOMBIA. Cauca: Valle de Las Papas, near Valencia, 2910 m, *Idrobo, Pinto & Bischler* 3643 (BM).

PERU. Huanuco: type as above; ibid. loc. 2650 m, *Asplund* 12843 (S).

Geographical range: Colombia and Peru.

123. Selaginella epirrhizos Spring in *Bull. Acad. r. Belg.* **10** : 229 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 218 (1850); Baker, *Fern Allies* : 81 (1887); Alston in Pulle, *Fl. Surin.* **1** : 167 (1938); Knox in *Trans. bot. Soc. Edinb.* **35** : 284 (1950). Type from French Guiana, Cayenne: *Leprieur* 12 (P).

Selaginella rigida Linden, *Catalogue* **8** : 15 (1853), nom. nud.; A. Braun, *Index Sem. Hort. bot., Berl.* Appendix **1857** : 22 (1857).

Selaginella affinis A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 296 (1865); Baker, *Fern Allies* : 63 (1887). Type from French Guiana.

Selaginella poeppigiana var. *guyanensis* Spring in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 218 (1850). Type from French Guiana.

Lycopodium plumosum sensu Aublet, *Hist. Pl. Guian.* : 967 (1775), non L. (1753).

Specimens seen:

FRENCH GUIANA. Without precise locality: *Aublet* s.n. (BM); *Leprieur* s.n. (K, P); type as above. Guyane: Bradel cataract, Rio La Comté, *Leprieur* 178 (P); Serra de Ouanari, *Black, Vincent & D'Aage* 17638 (BM, IAN).

SURINAM. Without precise locality: *Hostmann & Kappler* 3 (L). Nickerie: Upper Nickerie R, *Tulleken* 509 (L); Phaedra, *Voltze* s.n. (U). Sarramacca: Bergendaal, *Focke* 386 (U); between Pakka-pakka and Ebatop, *Florschütz* 1393 (BM). Suriname: Blaauwe Berg, *Splitgerber* 893 (L).

GUYANA. Without exact locality: Penal Settlement, *Guppy* 2 (BM); between Demerara and Berbice Rivers, *De La Cruz* 1606 (NY). Demerara: Malali, Demerara R, *De La Cruz* 2679 (K, NY); Demerara, *Andersen* 40 (BM). Essequibo: Kamuni Creek, Groete Creek, Essequibo R, *Maguire & Fanshawe* 22847 (BM); *Smith* 2108 (BM); Mt Arisaru, *Guppy* 28 (BM); Kaieteur Falls, *Appun* s.n. (BM); Head Falls, Mazaruni R, *Jenman* 645 (K), s.n. (NY); Mazaruni Station, *Sandwith* 1231 (BM); Kamakusa, Upper Mazaruni R, *De La Cruz* 2793 (NY); Camaria road, junction of Mazaruni and Caryuni Rivers, *Graham* 368 (BM, NY), 407 (BM, NY); near Lower Camaria *Tutin* 147 (BM); *Richards* 841 (BM, K); Bartica, *Hitchcock* 17257 (NY); Bartica Grove, *Jenman* 2326 (BM); Arawak Matope, Cuyuni R, *Tutin* 382 (BM); Rockstone, *Gleason* 685 (NY); Tiger Creek, Potaro R, *Jenman* s.n. (NY); Potaro Road, *Guppy* 7 (BM); Tumutumari, *Gleason* 57 (NY), 455 (NY), 456 (NY); *Hitchcock* 17379 (NY); *Linden* 29 (NY); *Tutin* 547 (BM); Kurupung, Mazaruni R, *Leng* 270 (NY); Sierra Acarai region, *c.* 3 km NE of Camp 1, *Guppy* 335 (BM); Takutu Creek to Puruni R, Mazaruni R, *Fanshawe* 1189 (NY), 2033 (BM); Kamuni Creek, Groete Creek, Essequibo R, *Fanshawe* 1821 (NY); Baracara, Mazuruni R, *Barkly* s.n. (BM); Upper Mazaruni, *De la Cruz* 2333 (NY), 2236 (NY), 2401 (NY); near Dadanawa, Upper Rupununi, *De La Cruz* 1811 (NY); Huradiaiah, Moruka R, Pomeroon District, *De La Cruz* 1019 (NY); Pomeroon R, *Jenman* s.n. (NY).

BRAZIL. Amazonas: S Francisco, Rio Acre, *Ule* 9141 (K).

Geographical range: The Guianas, extending into NW Brazil.

Notes: A form with smaller leaves occurs in Guyana. It has been seen from Tiger Creek, Potaro R, *Jenman* s.n. (NY); Tumatumari, Potaro R, *Hitchcock* 17379 (NY); Tiger Creek, Tumatumari, *Tutin* 544a (BM). The species has a characteristic appearance due to the imbricate leaves of the tapering terminal branchlets and regularly spaced lateral leaves of the main stem.

124. Selaginella poeppigiana (Spring) Spring ex Splitg. in *Tijdschr. Natuurl. Gesch. Physiol.* **7** : 443 (1840), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 217 (1850), p.p. quoad pl. andina; Baker, *Fern Allies* : 62 (1887), p.p.; Knox in *Trans. bot. Soc. Edinb.* **35** : 286 (1950). Type from Ecuador, Pichincha: *Jameson* s.n. (K).

Selaginella sulcata subsp. *poeppigiana* Spring in *Flora, Jena* **21** : 185 (1838). Type as above.

Lycopodium poeppigianum Hook. & Grev. in *Bot. Misc.* **3** : 106 (1833), p.p., non l.c. **2** : 393, No. 144 (1831).

Specimens seen:

ECUADOR. Pichincha: type as above. Santiago-Zamora: Quebrada Honda, *André* K 456 (K, NY); between Quebrada Honda and Tambo Valladolid, 2000–3000 m, *Steyermark* 54592 (BM).

PERU. Ancash: Pampayacu, *Kanehira* 182 (US). Cuzco: Paucartambo, Marcachea, near Achirani, *Vargas* 11147 (UC); Paucartambo, between Patria and Libertad, 650 m, *West* 7102 (UC). Junin:

Schunke Hacienda, above San Ramon, 14–1700 m, *Schunke* A 252 (BM, US), A 253 (BM); *Killip & Smith* 24657 (BM, NY); Chanchamgyo Valley, *Schunke* 192 (BM), 231 (BM); Pangoa, *Matthews* 1085 (K). Loreto: Monte Campana, near Tarapoto, *Spruce* 4626 (BM, CGE, NY).

Geographical range: Ecuador to Peru.

Notes: This species, because of the auricles on the lateral leaves, may perhaps be regarded as conspecific with *S. sulcata* (No. 129). If maintained as distinct this epithet presents a complicated problem of nomenclature. Hooker & Greville originally applied the name *L. poeppigianum* to a Cuban plant collected by Poeppig, but in 1833 included this species under *L. stoloniferum.* They write 'We find, upon examining authentic specimens of the *L. stoloniferum* of Swartz, in the Banksian Herbarium [i.e. in the British Museum], communicated by himself from Hispaniola, that we have committed an error in regard to the present plant. The species we named *L. Pœppigianum* is the true plant of Swartz, and was indeed transmitted to us as such by our friend Professor Kunze. The specific appellations of the two plants will, therefore, have to be transposed, and the synonyms of our *L. stoloniferum* referred to what we have erroneously called *L. Pœppigianum*'.

Hooker had two specimens from 'Demerara, *Parker* & Pichincha, *Jameson*'. In 1834 Kunze *(Linnaea,* **9** : 11) referred a plant from Pampayaco, *Poeppig* to this species; this has since been taken out as *S. kunzeana* (No. 114). In *Flora, Jena* **21** Spring makes it a subspecies of *S. sulcata* and notes three specimens: Peru: *Poeppig, Jameson* and Demerara: *Parker.* In his monograph, Spring made two varieties: *mexicana* (= *S. galeottii* Spring) and *guyanensis* (= *S. epirrhizos,* No. 123) evidently regarding the Andine plant as the type, which reduces the type to *Jameson*'s specimen in Hooker's herbarium (i.e., K).

125. Selaginella suavis (Spring) Spring in *Bull. Acad. r. Belg.* **10** : 229 (1843), *Mém. Acad. r. Sci. Lett. Belg.* **24** : 216 (1850). Type from W. Brazil, without exact locality, *Sellow* s.n. (B, K).

Selaginella sulcata subsp. *suavis* Spring in *Flora, Jena* **21** : 185 (1838); in Martius & Endl., *Fl. Bras.* **1** (2) : 131 (1840). Type as above.

Selaginella glaziovi Fée, *Crypt. Brés.* : 232 (1869); *l.c. Suppl.* : 101 (1873). Type from Brazil.

Specimens seen:

PERU. Junin: Tarma, San Ramon, Valle de Chanchamayo, 800–900 m, *Constance & Tovar* 2269 (UC).

BRAZIL. Without exact locality: type as above (BM fragment = *S. sulcata* (No. 129) [det. Somers]). Espiritu Santo: Serra da Caparao, 1550 m, *Mexia* 4072 (BM). Mato Grosso: Esperidras, *Hoehne* 733 (BM). Minas Gerais: Cel-Pacheco, *Heringer* 1522 (BM). Rio de Janeiro: *Glaziou* 4482 (C, K), 4502 (C, K); Corcovado, *Didrichsen* 3135 (C); Monte Serrat, near Itatiaya, *Rose & Russell* 20440 (NY, P); Itatiaia, *Dusen* 654 (BM); *Brade* 10048 (BM); Santa Magdalena, 1000 m, *Lima & Brade* 13189 (BM). Santa Catarina: *Schreiner* s.n. (BM). São Paulo: Serra da Cantareira, *Loefgren* 530 (BM), 12 (C, S), 168 (P).

Geographical range: Brazil and reaching central Peru in the west.

Notes: There is confusion over the typification of this taxon. Spring (1838 : 185) refers to *Lycopodium marginatum* of Gaudichaud in Freycinet, *Voyage Autour Monde, Bot.* : 286 (1828) which refers to a Brazilian plant (Rio de Janeiro: calçada da Estrella). Gaudichaud's specimens at K (fide Alston (1936) et nostra) and at B (Somers, pers. comm.) is *S. sulcata* (No. 129). In *Fl. Bras.* Spring began to emend the description, mentioning *L. marginatum* [sensu] Gaud. in synonymy, but lists other Brazilian specimens the first of which is Sellow (*in Brazilia meridionali*) and may be selected as type, although the fragment at BM suggests a mixed gathering and further adds to the confusion.

126. Selaginella silvestris Asplund in *Ark. Bot.* **20A** : 30 (1926). Type from Bolivia, La Paz: El Chaco, Sur Yungas, *Asplund* 1140 (BM (fragment); UPS; Herb Birger).

Selaginella poeppigiana sensu Baker, *Fern Allies* : 62 (1887), p.p. non Spring (1838 & 1840); Hieron. *Bot. Jb.* **34** : 581 (1905).

Specimens seen:
COLOMBIA. Antioquia: Palmitas, *Skolnik, Daniel & Barkley* 19 An 158 (BM). Caldas: Rio Santa Rita, Salento, 1600–1800 m, *Killip & Hazen* 8991 (NY), 10137 (NY). Caqueta: Balsillas Mts, *Ariste-Joseph* s.n. (US). Cauca: Canaan, Mt Pirace, 3100–3300 m, *Pennell & Killip* 6687 (BM, NY); near Popayan, 1800 m, *Alston* 8023 (BM). Cundinamarca: Tocarema, 2500 m, *Lindig* 1508 (BM); between La Vega and Facatativa, 2100 m, *Haught* 6163 (BM); La Esperanza, *Pérez Arbeláez* 2576 (COL). Norte de Santander: Paramo de Fontibon, Pamplona, 2400 m, *Alston* 7128 (BM); La Mesita, Pamplona, 2725 m, *Alston* 7235 (BM); Loso, N of Toledo, 2200–2400 m, *Killip & Smith* 20402 (NY). Putumayo: near Lake Cocha, 2700 m, *Alston* 8309 (BM); near Llorente, E of Quebrada Balsal, 2290 m, *Ewan* 16260 (BM); Valle de Sibundoy, 1·5 km NE Sibundoy, *c.* 2200 m, *Bristol* 443 (COL). Santander: near La Baja, 3000 m, *Killip & Smith* 18114 (NY), 18357 (NY). Tolima: Quebrada Peralis, Quindin Road, 2600 m, *Alston* 7753 (BM).
ECUADOR. Without precise locality: *Spruce* 4785 (BM, CGE, NY). Azuay: near Servilla de Oro, 2440–2745 m, *Camp* E 4285 (BM). Guyas: 3 km W of Bucay, Teresita, 270 m, *Hitchcock* 20423 (NY). Manabi: Monte Christi Hill, *Fagerlind & Wibom* 509 (S). Napo-Pastaza: near La Chonta, *Rose* 23467 (NY); road Baeza-Lago Agrio, 23 km from Baeza at Rio Oyacachi, 1500 m, *Balslev & Madsen* 10451 (BM). Pichincha: Nono-Gualea, *Sodiro* s.n. (NY); Tandapi, 2000 m, *Mille* s.n. (NY); Quito, *Jameson* 28 (BM); Cerro Carazon, *Camp* E 1667 (BM); San Florencio, 1580 m, *André* 3655 (NY); Pichincha, *Sodiro* s.n. (NY); Chaupi-Sagcha, Pululagua, 1830 m, *Bell* 436 (BM). Tungurahua: Cusatanga near Ambato, *Pachano* 176 (US).
PERU. Cuzco: Keros Valle Cosnipata, 950 m, *Scolnik* 895 (BM); between Mistiana and Keros, 650 m, *Vargas* 7398 (BM); Valle de Santa Anna, prov. Convencion, *Herrera* 3009 (US); Convencion, Potrero, 8 m W of Quillabamba, 1200 m, *R. & A. Tryon* 5394 (BM). Huanuco: Carpish Divide, 2650 m, *Sandeman* 5118 (BM); *Asplund* 12842 (S). Junin: Perene River, 1190 m, *Gascoyne-Cecil* 90 (BM).
BOLIVIA. La Paz: type as above; Sirupaya near Yanacadis, Sur Yungas, 1650 m, *Buchtien* 441 (US); San Felipe Unduavi, 2650 m, *Buchtien* 11367 (US).

Geographical range: Guatemala southwards to Bolivia.

Notes: This species is very close to *S. trisculcata* (No. 127), but the oblong lateral leaves are rounded at the apex, and only toothed towards the base.

127. Selaginella trisulcata Asplund in *Ark. Bot.* **20A** : (1926); Knox in *Trans. bot. Soc. Edinb.* **35** : 286 (1950). Type from Bolivia, La Paz: El Chaco, Sur Yungas, 1900 m, *Asplund* 1482 (S, holotype; UPS, Herb Birger, isotypes).
Selaginella buchtienii Hieron. in *Meded. Rijks-Herb* **27** : 2 (1915), nom. nud.
Selaginella poeppigiana var. *peruviana* A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 295 (1865).

Specimens seen:
ECUADOR. Napo: Cuyuja, S of Rio Papallacta, 2500–2650 m, *Balslev & Madsen* 10540 (AAU, BM).
PERU. Ayacucho: Aina, between Huanta and Rio Apurimac, 750–1000 m, *Killip & Smith* 22751 (BM, NY); Carrapa, between Huanta and Rio Apurimac, 1500 m, *Killip & Smith* 22359 (BM, NY). Cuzco: San Miguel, Urubamba Valley, 1800—2300 m, *Herrera* 2024 (BM); *Cook & Gilbert* 878 (NY, US); Aobamba, Huadquiña, prov. Convencion, *Vargas* 8154 (BM). Huanuco: Carpish Pass, 2750 m, *Allard* 20996 (BM). Junin: Oxapampa, prov. Pasco, 1600 m, *Soukup* 3359 (BM); Carpapata, above Huacapistana, 2400 m, *Killip & Smith* 24373 (BM, NY); 2700–3200 m, *Killip & Smith* 24467 (BM, NY); Huacapistana, 1800 m, *Killip & Smith* 24309 (BM, NY); Schunke Hacienda, above San Ramon, 1300–170 m, *Schunke* H 253 (US); Chanchamayo, *Schunke* s.n. (BM); Pichis trail, Yapas, 1350–1600 m, *Killip & Smith* 25588 (BM, NY).
BOLIVIA. Without precise locality: *Bridges* s.n. (BM); *Bang* 51 (BM), 66 (BM). Cochabamba: Antahuanca, Quebrada del Rio Espiritu Santo, 750 m, *Buchtien* 2255 (US); *ed. Rosenstock* 92 (BM); Incahaca, 2440 m, *Brooke* 6659 (BM). La Paz: type as above; near Yungas, *Bang* 577 (BM, NY, US); 1830 m, *Rusby* 452 (NY, US); Polo-Polo, near Coroico, N Yungas, 1000 m, *Buchtien* 3550 (US); *ed. Rosenstock* 101 (BM), 4847 (US); Unduavi, 2440 m, *Rusby* 454 (NY); Yungas, Caranavi, *Ellenberg* 6223 (AAU); Sur Yungas, Chulumani, 2135 m, *Brooke* 6531 (BM).
BRAZIL. Para: vicinity of Cachoeira, km 96, road BR22, Capanema to Maranhão, Varzea forest, *Prance & Pennington* 1866 (BM).

Geographical range: Ecuador, Peru, Bolivia, with an outlier in mid-Brazil.

128. Selaginella sericae A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 298 (1865); in *Mber. K. preuss. Akad. Wiss.* **1865** : 187 (1866); Baker, *Fern Allies* : 82 (1887). Type from Ecuador, without exact locality: Andes of Quito, *Cuming* 82 (B).

Selaginella sericea var. *latifolia* A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 298 (1865). Type from Ecuador.

Selaginella sericea var. *elongata* Sodiro, *Rec. Crypt. Vasc. Prov. Quito* : 94 (1883), *Crypt. Vasc. Quito* : 613 (1893). Type from Ecuador.

Specimens seen:
ECUADOR. Without precise locality: type as above; *Spruce* 4786 (BM, CGE, NY); *Jameson* s.n. (K); *Fraser* s.n. (BM). Guayas: between Hacienda Chontal and Santa Elena, 1035–1400 m, *Camp* E 812 (BM). Pichincha: Nanegal, *Sodiro* s.n. (K); Mondo, *Sodiro* s.n. (K); San Florencio, 1580 m, *André* 3640 (K, NY); near Chiriboga, 1900–2000 m, *Fagerlind & Wibom* 1932 (S). Santiago-Zamora: between Rio Sabanilla and Cannilones Tambo, 1370–2135 m, *Camp* E 63 (BM); near Mendez, *Camp* E 4941 (BM); between Rio Sordo and la Esperanza, 2000–2600 m, *Acosta Solis* 7353 (BM). Tungurahua: *Asplund* 17400 (S); Hacienda Rio Verde Grande, 1500 m, *Asplund* 7857 (S).

Geographical range: confined to Ecuador.

129. Selaginella sulcata (Desv.) Spring ex Martius in *Flora, Jena* (Beibl.) **1837** (2) : 126 (1837); Baker, *Fern Allies* : 63 (1887), excl. syn. A. Braun; Knox in *Trans. bot. Soc. Edinb.* **35** : 286 (1950). Lectotype from Brazil: without exact locality. in herb *Desvaux* (P); apud. P. Somers, pers comm.

Lycopodium sulcatum Desv. ex Poiret *Encl. Suppl.* **3** : 549 (1814); Sprengel, *Syst. Veg.* **4** : 19 (1827). Lectotype as above.

Lycopodium stoloniferum sensu Raddi, *Pl. Bras. Nov. Gen.*: 81 (1825), non Sw. (1788).

Selaginella lorentzii Hieron. in Engl., *Bot. Jahrb.* **22** : 419 (1896). Type from Argentina.

Selaginella sulcata var. *cruenta* Martius in *Flora, Jena* (Beibl.) **1837** (2) : 126 (1837). Type from Brazil.

Selaginella rubescens Hieron. in *Hedwigia* **43** : 236 (1904). Syntypes from Brazil.

Selaginella caudorrhiza Baker in *J. Bot., Lond.* **21** : 334 (1883), *Fern Allies* : 59 (1887); Alston in Pulle, *Fl. Surin.* **1** : 167 (1938); Knox in *Trans. bot. Soc. Edinb.* **35** : 284 (1950). Type from Surinam.

Selaginella biauriculata Hieron. in Engl. & Prantl, *Nat. Pflanzenf.* **1** (4) : 711 (1901). Type from Brazil.

Selaginella sulcata var. *biauriculata* Hieron. ex Bonap., *Notes Ptérid.* **2** : 140 (1915). Type from Brazil.

Specimens seen:
SURINAM. Without exact locality: *Hostmann* 3 (BM, K, type of *S. caudorrhiza* Baker).

BOLIVIA. Cochabamba: Antahuacana, Espiritu Santo, N of Cochabamba, 750 m, *Buchtien* s.n. (Rosenstock exsicc. 97; BM), *Buchtien*, 2253 (US); Espiritu Santo, near Cochabamba, *Bang* 1287 (BM, NY, US). La Paz: Hacienda Simaco, Tipuani, 1400 m, *Buchtien* 5281 (US), 5282 (BM, US), 5285 (BM, NY, US); Bopi River, 915 m, *Rusby* 392 (NY, US); Huachi, Beni River, 1800 m, *White* 540 (NY, US); Tumupasa, 550 m, *Williams* 1405 (NY, US); Polo-Polo, near Corvico, *Buchtien* s.n. (BM), 3556 (BM); Mapiri, Larecaja, 1525 m, *Rusby* 462 (NY). Santa Cruz: Buena Vista, Sara province, 400 m, *Steinbach* 5522 (BM, NY, US), 2068 (BM).

BRAZIL. Without exact locality : type as above; *Swainson* s.n. (K); *Lobb* s.n. (BM, K); *Glaziou* 461 (C), 2277 (C), 3544 (C), 4490 (BM, C, K, P), 4502 (B), 4503 (C), 5639 (P), 7302 (C), 7356 (C), 7966 (C, P), 13366 (C, P), 14415 (C, P); *Burchell* 2238 (K); *Sellow* 73b (BM); *Bowie & Cunningham* s.n. (BM); *Barclay* 142 (BM). Amazonas: *Glaziou* s.n. (BM). Bahia: *Blanchet* 2207 (P). Ceará: Ubuassú, *Dias* s.n. (BM); Baturité, Santa Clam, *Leite* 1359 (BM). Espirito Santo: Caparaó, *Schwacke* s.n. (BM); Serra de Caparaó, *Schwacke* s.n. (BM); Jatiboca, *Brade, Altamiro & Apparicio* 18445 (BM); Cachoeiro do Itapemirim Faz, Ito. Antonio da Pedra Branca, *Brade* 19371 (BM). Matto Grosso: Guia, *Lindman* A 3493 (NY); *H. Smith* 147 (BM). Minas Geraes: Fazenda de Grama, Carangola distr., *Mexia* 4263 (BM); *St Hilaire* 1430 (P); Angra ds Reis, *Hoehne* 17417 (BM); Serra do Angico, Fazenda do Diamante, *Mexia* 5644 (BM). Paraiba: Areia, *Vasconcellos* 260 (BM). Parana: Serra do Mar, *Dusen* 3797 (BM, P), 15243 (C), 14375 (C). 609a (C); Rio Branco, *Dusen* s.n. (BM); Lucena, *Wielewski* s.n. (NY), 3 (NY), 11

(BM); San Mattheus, *Gänsly* 15 (NY); São João, 545 m, *Dusen* 15423 (BM); Iguazu, *Beetle* 2054 (BM). Pernambuco: *Pickel* 60 (S); Tapera, *Pickel* 55 (BM, US). Rio Janeiro: *Gaudichaud* s.n. (K); *Glaziou* s.n. (BM); *Forbes* s.n. (BM); *Gardner* 65 (BM); *Mertens* s.n. (BM); *Du Parquier* s.n. (BM); *Gaudichaud* 135 (C); *Leprieur* 199 (C); *Mosen* 52 (C); *Warming* 1863 (C); *Regnell* 298 (C); Corcovado, *Martius* 197 (M); *Raddi* s.n. (B); *Jameson* s.n. (B, BM); *Glaziou* 4490 (BM); *Brade* s.n. (BM); Serra Estrella, near Mandiocca, *Riedel* s.n. (K); Nova Friburgo, *Glaziou* 17961 (C, P, type of *S. biauriculata* Hieron.) Tijuca, Estrada D. Castorina (Gavea) a vista Chinesa, *Alston & Lutz* 347 (BM). Districto Federal: *Lutz* 1650 (BM); Sugar Loaf Hill at entrance to harbour of Rio de Janeiro, *Jameson* s.n. (BM); Teresopolis, *Sampaio* 2688 (BM); Averuda Niemeyer, *Freire & Vidal* s.n. (BM); Mattas do Rio Frapicherro, *Peckolt & Freire* 617 (BM); Gavea, *Frazao* s.n. (BM); Nictheroy, Frubuky, *Brade* 12833 (BM), 15717 (BM). Rio Grande do Sul: Irai ad flumen Uruguay superius, *Emrich* s.n. (BM); Taquara, Caracol, *Dutra* 1611 (BM); Porto Novo, ad ripam fluminis Uruguay, *Dutra* 687 (BM). Santa Catarina: Joinville, *Schmalz* 152 (NY); *Mueller* 138 (BM, NY); Lages, *Spannagel* 13 (NY); Itapiranga-Chapecó, *Reitz* 3861 (BM); Hapiranga, ad fluminis Uruguay-Peperi, *Rambo* 49819 (BM). São Paulo: Campinas, *Novaes* 7418 (BM); Ypiranga, *Luederwaldt* 1659 (BM), 7644 (BM); Guaruja, Santos, *Usteri* 21024 (S), 21032 (S); Cantareira, *Brade* 5138 (NY); Iguape, Morro das Pedra, *Brade* 15718 (BM).

Geographical range: Surinam and French Guiana (Somers, pers. comm.), Bolivia to south Brazil, Argentina and Paraguay.

Notes: S. sulcata is distinguished from all the other prostrate species with articulate stems by the two long straight eciliate auricles of the axillary leaves. The lateral leaves have long finger-like, eciliate auricles on the upper side. The auricles in *S. diffusa* (No. 133) are more deflexed and usually long-ciliate.

130. Selaginella horizontalis (C. Presl) Spring in *Bull. Acad. r. Belg.* **10** : 226 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 264 (1850); A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 292 (1865), in *Mber. K. preuss, Akad. Wiss.* **1865** : 187, 194 (1866); Knox in *Trans. bot. Soc. Edinb.* **35** : 285 (1950); Alston in *J. Bot., Lond.* **72** : 226 (1934). Type from Peru, *Haenke* s.n. (PR).

Lycopodium horizontale C. Presl, *Rel. Haenke* : 78 (1825). Type as above.

Selaginella suavis var. *haenkeana* Spring in *Flora, Jena* **21** : 197 (1838). Type from Peru.

Selaginella fendleri Baker in *J. Bot., Lond.* **21** : 334 (1883), *Fern Allies* : 59 (1887). Type from Panama.

Specimens seen:

VENEZUELA. Apure: Llanos de l'Apure, *Geay* s.n. (P). Aragua: San Juan de los Morros, 400 m, *Alston* 6034 (BM), 6050 (BM). Carabobo: Carobobo, 500 m, *Alston* 5606 (BM); Cojedes: near San Carlos, *Alston* 6306 (BM); Aguarita, between Tinaquillo and San Carlos, *Alston* 6319 (BM); near Acarigua, *Alston* 6320 (BM). Zulia: near El Vigia, Rio Chama, *Vareschi & Pannier* 1653 (BM).

COLOMBIA. Antioquia: Mulatos, 50 m, *Haught* 4869 (BM, C); Rio Ampurrumiadó, 200 m, *Gutierréz & Barkley* 17c199 (S). Cauca: Carretera a la Plata, de Puracé al Alto de San Rafael, 2660–3450 m, *Garcia-Barriga & Hawkes* 12869 (COL). Chocó: Saltos de Truando, *Schott* s.n. (BM, NY, US); Quibdo, Rio Atrato, 60 m, *Archer* 1805 (BM); Ciudad Mutis (Bahia Solano), 5 m, *Pinto & Kotschwar* 131 (COL); Negria, *c.* 50 m, *Killip* 35023 (COL); between Quebrada Guarapo and Mandinga, 120–180 m, *Killip* 35197 (COL). Magdalena: Caño Blanco, SE of La Jagua, foot of Sierra Perija, 200 m, *Haught* 3629 (BM); Santa Marta, *von Rohr* 89 (BM); Agua Dulce Road, Santa Marta, 305–1065 m, *Smith* 2238 (BM, NY, US); Don Diego, near sea level, *Smith* 2699 (NY, US); Rio Frio, Santa Marta, *O'Neill* 1245 (US). Meta: Guatiquia, near Villavicencio, 500 m, *Alston* 7592 (BM); near El Mico Airstrip Rio Guejar, 400 m, *Philipson, Idrobo & Fernandez* 1373 (BM). Putumayo: Mocoa, 550–730 m, *Schultes & Cabrera* 19062 (US); near Puerto Asis, 375 m, *Ewan* 16759 (BM). Valle del Cauca: bridge over Dagua, near Buenaventura, *Alston* 8610 (BM); Buenaventura, *Wall* s.n. (S); Rio Dagua, near Cordoba, *Killip* 5045 (NY, US), 5049 (US); Santa Rosa to Villa Cisneros, 250–350 m, *Killip* 5365 (US).

ECUADOR. Pastaza: Mera, along Rio San Jorge and Rio Tigre, 1200 m, *Øllgaard & Balslev* 9203 (AAU, BM).

Geographical range: Costa Rica southwards to Peru.

Notes: S. horizontalis is most readily separated from *S. humboldtiana* (No. 132) by the long cilia on the auricles of the lateral leaves. In the dry season contracted stems with crowded thicker leaves are produced at the tips of normal stems. The apices of the stem are often ascending which is apparent from dried material by the descending rhizophores.

131. Selaginella microtus A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 293 (1865). Type from Ecuador, Guayas: Balao, Guyaquil, *Jameson* 374 (BM, G).
Selaginella lingulata sensu Baker, *Fern Allies* : (1887), p.p. non Spring (1850).

Specimens seen:
COLOMBIA. Meta: Puerto Lopez, intendencia del Meta, 240 m, *Little* 8389 (BM). Valle del Cauca: bridge over Rio Dagua, near Buenaventura, *Alston* 8658 (BM).
ECUADOR. Without exact locality: *Fraser* s.n. (BM). Guayas: type as above; Guyaquil, *Hall* s.n. (K); between the airport and textile factory San Antonio, Guyaquil, *Asplund* 20413 (S). Los Rios: Hacienda Clementina, Rio Pita, *Asplund* 5264 (S), 5332 (S); Junction of provinces Guayas, Cãnar, Chimborazo and Bolívar: foothills of W Cordillera, near Bucay, 305—460 m, *Camp* E3709 (BM).

Geographical range: Colombia and Ecuador.

Notes: The median leaves of the main stem in *S. microtus* are broadest above the middle, abruptly acuminate at the apex, and constricted at the base of the shortly ciliate auricle, which is half as long as the lamina and peltate. In *S. diffusa* (No. 133) the median leaves are broadest about the middle, gradually acuminate, at the apex, and less constricted at the base of the long-ciliate, but smaller, auricle. The median leaves of *S. microtus* normally show two unequal auricles. Moreover, the lateral leaves appear as if attached to the lower surface of the main stem, whereas in *S. microtus* they are inserted laterally.

132. Selaginella humboldtiana A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 293 (1865). Type from Venezuela, without exact locality: Orinoco, *Humboldt* s.n. (B, fragment at BM).
Selaginella sulcata var. *cruenta* sensu Baker, *Fern Allies* : 63 (1887), p.p. quoad syn. A. Braun.

Specimens seen:
VENEZUELA. Without exact locality: type as above.
COLOMBIA. Antioquia: Virginias, 40 km E of Puerto Berrio, *Archer* 1449 (BM, US); Isletas, Rio Nare, *André* 436 (NY). Choco: Andagoya, 70–100 m, *Killip* 35489 (COL). Magdalena: Africa, Sierra Perija, 1500 m, *Haught* 4491 (BM). Norte de Santander: near La Esmeralda, 750 m, *Killip & Smith* 20934 (NY). Santander: near Barranca Bermeja, *Haught* 2014 (BM). Tolima: Mariquita, bosque del Acueducto, 550 m, *Murillo* 15 (COL).

Geographical range: Venezuela and Colombia.

Notes: This species is distinguished from *S. diffusa* (No. 133) by the median leaves, which are distinctly aristate and have a single, more or less peltate, auricle. The lateral leaves are only shortly ciliate at the base and have two short auricles, the lower slightly longer than the upper.

133. Selaginella diffusa (C. Presl) Spring in *Bull. Acad. r. Belg.* **10** : 143 (1843), in *Mém. Acad. r. Sci. Lett. Belg.* **24** : 104 (1850); A. Braun in *Mber. K. preuss. Akad. Wiss.* **1865** : 203 (1866); Alston in *J. Bot., Lond.* **72** : 226 (1934). Type from Panama, without exact locality, *Haenke* s.n. (B).
Lycopodium diffusum C. Presl, *Rel. Haenk.* : 78 (1825). Type as above.
Lycopodium mnioides Sieber ex Hook. & Grev. in *Bot. Misc.* **2** : 394 (1831). Type from Trinidad.
Selaginella mnioides (Sieber) Spring in *Bull. Acad. r. Belg.* **10** : 228 (1843), non sensu Hieron. (1905). Type as above.
Selaginella ciliauricula Spring ex Klotzsch in *Linnaea* **20** : 436 (1847), nom. nud., *Mém. Acad. r. Sci. Lett. Belg.* **24** : 219 (1850). Type from Venezuela.

Selaginella cirrhipes Spring ex Klotzsch in *Linnaea* **20** : 436 (1847), nom. nud., *Mém. Acad. r. Sci. Lett. Belg.*, **24** : 221 (1850). Type from Venezuela.

Selaginella mnioides var. *major* A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 301 (1865). Type from Venezuela.

Selaginella mnioides var. *minor* A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 301 (1865).

Selaginella macrophylla A. Braun in *Annls Sci. nat.* (Bot.) V, **3** : 302 (1865). Type from Bolivia.

Selaginella polycephala Baker in *J. Bot., Lond.* **21** : 332 (1883). Type from Colombia.

Selaginella anisotis Sodiro, *Recens. Crypt. Vasc. Prov. Quito* : 94 (1883). Type from Ecuador.

Selaginella eggersii Sodiro, *Crypt. Vasc. Quito* : 605 (1893). Type from Ecuador.

Specimens seen:

VENEZUELA. Aragua: North slope, near La Cumbra, Parque Nacional 800 m, *Alston* 5789 (BM); cloud forest of Rancho Grande, 100 m, *Williams & Alston* 168 (BM, UC); Mts N of Maracay, on Choroni Road, 1200–1300 m, *Box* 3930 (BM); Choroni Road Summit, 1500 m, *Box* 3964 (BM); Parque Nacional near Rancho Grande, 800–1000 m, *Killip* 37128 (BM). Merida: Los Andes, *Moritz* 380 (B, BM, type of *S. ciliauricula* Spring and *S. mnioides* var. *major* A. Braun); Jaji, near Ejido on a bank, 1500 m, *Alston* 6985 (BM); Rio Albariga, N of Merida in forest, 2400 m, *Alston* 6961 (BM); Merida, 1400 m, *Alston* 6668 (BM); 4·8 km W, 3·2 km S of Merida, 1370 m, *Reed* 425 (BM). Miranda; Caracas, *Ernst* 1717 (BM); Galipan, *Moritz* 379 (B, BM, type of *S. cirrhipes* Spring). Tachira: Palo Grande, 1450 m, *Alston* 7100 (BM). Trujillo: between Valera and Timotes, 1000 m, *Alston* 6510 (BM).
COLOMBIA. Without exact locality: *Lehmann* 87 (BM). Antioquia: 4 km al ceste de Palmitas, 1700 m, *Barkley, Gomez & Gomez* 427 (BM); 20 km W of Medellin, *Constantino, Lopez & Ayerve* 429 (BM); environs of Bocaná, 1900 m, *Molina, Molina & Molina* 352 (BM); Medellin, 1500 m, *Archer* 1350 (BM); Salto de Guadalupe, 1600 m, *Hodge* 6950 (BM); environs of Angelopolis, 1950 m, *Gutiérrez & Barkley* 17C 648 (COL); Jerico, 1970 m, *Tomas & Daniel* 3372 (COL); Narino, 1500–1900 m, *Uribe* 2131 (COL); Titiribi, 170 m, *Archer* 570 (US); environs of Sonsón, *Molina & Barkley* 18A352 (COL); Region de Rioverde, Sonsón, *Gutiérrez* 35609 (UC); Amaya, *Daniel* 4252 (BM); Medellin, 2000 m, *Archer* 1517 (BM). Boyaca: Labranzgrande, 1150 m, *Amórtegni* 346 (US); around Bocota, *c.* 2200 m, *Grubb & Guymer* P 80 (BM, COL). Caldas: Rio Santa Rita, Salento, 1600–1800 m, *Killip & Hazen* 9005 (BM, US); Cordillera Central, Salento, 1600–1800 m, *Killip & Hazen* 8849 (US); Rio Quindio above Armenia, 1300–1500 m, *Pennell, Killip & Hazen* 8705 (US), 8705a (US); Medellin River Valley, near Caldas, 1700–1800 m, *Hodge* 6658 (BM). Caqueta: Florencia, *Arbelaez* 622 (BM, US). Cauca: Dagua, *Arbelaez* 3205 (BM); Carretera a La Plata, de Puracé al Alto de San Rafael, 3450–2660 m, *Garcia & Hawkes* 12869 (BM). Cundinamarca: Camino de herradura antiguo de Guadas a Honda: del valle de Guaduas al Alto de Ficalito, 1200–1700 m, *Garcia-Barriga* 11873 (BM); Bogata, Herb. *Triana* 696 (BM); near falls of Tequendama, *Ariste-Joseph* A907 (US). Huila: 0·5 km NE of Algeciras, 1005 m, *Little* 9267 (COL); west of 'Balsillas', 2000–2300 m, *Rusby & Pennell* 910 (US); Canyon of Rio Neiva, NE of Algeciras, 1830 m, *Little* 9283 (COL); 25–40 km SE of Neiva, canyon of Rio de Las Ceibas, 1950 m, *Little* 9305 (COL); Hoya del Magdalena, San Agustin, 1860 m, *Idrobo, Pinto & Bischler* 2916 (COL). Magdalena: Santa Marta, *H. H. Smith* 2685 (BM, US), 2238 (BM); *Purdie* s.n. (BM, K; type of *S. ciliauricula* Spring); Sierra Nevada de Santa Marta, region del Campano, 1300 m, *Barkley & Gutiérrez* 1903 (BM); around San Andrés de la Sierra, western slope of Cordillera de Santa Marta, 1100–1300 m, *Pittier* 1710 (US); Mt San Lorenzo, near Santa Marta, 1900–2400 m, *Seifriz* 180 (US); 'Cincinnati', lower slopes of Mt San Lorenzo, near Santa Marta, 1300 m, *Seifriz* 34 (US); between Pueblo Viejo and San Miguel, 900—1700 m, *Seifriz* 337 (US). Nariño: Ricaurte, between Pasto and Tumaco, *Espinosa* E2921 (BM), E2923 (BM); Rio San Juan near junction of Rio San Juan drainage, Rio Puelmambi, 1540 m, *Ewan* 16039 (BM). Putumayo: Rio Ticuanayoy at confluence of Rio Caqueta, Cordillera Oriental, 1100 m, *Ewan* 16802 (BM). Santander: Ocãna, *Schlim* 493 (BM); between El Roble and Tona, 1500–1900 m, *Killip & Smith* 19428 (US); between Piedecuesta and Las Vegas, 2000—2500 m, *Killip & Smith* 15551 (US). Tolima: Mariquita, Herb. *Triana* 696 (BM): 'La Trinidad', Libano, 1100–1300 m, *Pennell* 3314B (US). Valle del Cauca: Cordillera occidental, 1600—2000 m, *Killip* 5585 (BM); 1800—2100 m, *Killip* 5550 (BM, US); Santa Rosa to Cisneros, Dagua Valley, *Killip* 5351a (US); La Cumbre, Cordillera Occidental, 1700—2100 m, *Killip & Hazen* 11128 (US); 1500—1700 m, *Hazen* 11842 (US); 1800—2200, *Killip* 5585 (US). Vaupés: Rio Negro, San Felipe and vicinity (below confluence of Rio Guainia and Rio Casiquiare), 185 m, *Schultes, Baker & Cabrera* 18296 (COL).

ECUADOR. Without exact locality: *Fraser* s.n. (BM); Andes Quitenses, *Jameson* 351 (BM); Andes Quitenses, *Spruce* 5603 (BM); Valle Takatanga, *Sodiro* s.n. (US, isotype of *S. eggersii* Sodiro). Cañar: Valley of Rio de Cañar, near Rosano, 1355 m, *Prieto* CP–26 (BM); Chimborazo Red Bark woods, *Spruce* 5677 (BM). El Oro: Moro-Moro region (about 34 km W of Portovelo), 1035–1280 m, *Camp* E 617 (BM). Guayas: Guayaquil, *Pearce* s.n. (BM). Pichincha: Cerro Corazon, *Camp* E 1666 (BM).
PERU. Cuzco: Paucartambo, between Santa Isabel and Consuelo, 1000 m, *Vargas* 7347 (BM); between Santa Isabel and Mistiana, Valle de Cosnipata, Paucartambo, 950 m, *Scolnik* 920 (BM). Huanuco: Churubamba, Hacienda Exito, bank of Rio Ysabel, 1100 m, *Mexia* 8133a (BM); Churubamba, Hacienda san Carlos; trail above Rio Ysabel, 1090 m, *Mexia* 8256 (BM); Tingo Maria, 700 m, *Tryon* 5227 (BM). Junin: La Merced, 700 m *Killip & Smith* 23543 (BM); Schunke Hacienda, above San Ramon, 1400–1700 m, *Killip & Smith* 24637 (BM), 24655 (BM), 24810 (BM); E of Quimiri Bridge, near La Merced, 800–1300 m, *Killip & Smith* 23949 (BM); Chanchamayo Valley, *Schunke* 196 (BM), 197 (BM); 1200 m, *Schunke* 230 (BM). San Martin: Tingo Maria, Las Cueras de los Pavos on road to Lima, 625–1100 m, *Allard* 20533 (BM); Tingo Maria, 625–1100 m, *Allard* 20846a (BM).
BOLIVIA. Without exact locality, *Kelly* s.n. (BM); *Bang* 909 (BM); *Orbigny* s.n. (P, type of *S. macrophylla* A. Braun). Cochabamba: Espiritu Santo, *Buchtien* s.n. (BM); Antahuacana, 750 m, *Buchtien* 2256 (US), 2254 (US). La Paz: Tipuani Valley, Hacienda Casana, 1400 m, *Buchtien* 7093 (US); Hacienda Simaco, above road to Tipuani, 1400 m, *Buchtien* 5284 (US); Chanopampa, Mapiri, 570 m, *Buchtien* 1024 (US); San Carlos, Mapiri, 750 m, *Buchtien* 1077 (US), 1076 (US); San Antonio, Mapiri, 870 m, *Buchtien* 1122 (US).

Geographical range: Costa Rica south to Bolivia on the Andes Range, and east to Trinidad and Surinam (Somers, pers. comm.).

Notes: A widespread species, very variable in its gross morphology and general habit. The leaf shape, size, and degree of ciliation are particularly variable. Somers, who has studied a wider range of specimens, states that the characteristic of this group is the biauriculate median leaves and multicellular cilia on the leaf margins.

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